TIMBER

AND

SOME OF ITS DISEASES

NATURE SERIES

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SOME OF ITS DISEASES

BY

H. MARSHALL WARD, M.A., F.R.S., F.L.S.

LATE FELLOW OF CHRIST'S COLLEGE, CAMBRIDGE; PROFESSOR OF BOTANY AT THE ROYAL INDIAN ENGINEERING COLLEGE, COOPER'S HILL

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PREFACE.

THE following attempt at a popular exposition of a subject almost unknown in this country, originated in a series of short articles in *Nature*, and when the publishers proposed that I should add to these and cast them into the form of a book, I assented with the more pleasure because it afforded an opportunity of calling attention to several points well worth further investigation.

Had my primary object been to write a treatise on the whole subject of the diseases of trees, I should have adopted a somewhat different plan, and discussed many of the phenomena at greater length.

Chapter IV. will perhaps be regarded as too technical for the general reader, but it seemed

better to bring the whole controversy forward, and make it tell its own story, because, so far as I am aware, no account of the matter has as yet been put before the English student, and so many points of interest turn up by the way.

No author could well approach the subject of the diseases of timber without consulting the works of De Bary and R. Hartig; nor attempt to classify woods without referring to the labours of Nördlinger and Gamble in addition: to these, and to the writings of Frank, Sorauer, Willkomm, Hesse, and others, I take this opportunity of acknowledging many obligations.

Cooper's Hill, 1889.

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TIMBER

AND

SOME OF ITS DISEASES.

CHAPTER I.

TIMBER, ITS GENERAL CHARACTERS AND STRUCTURE.

On carefully examining the clean-cut end of a sawn log of timber, it is easy to convince ourselves of the existence of certain marks upon it which have reference to its structure. These marks will vary in intensity and number according to the kind of tree, the age at which it is felled, and some other circumstances, which may be overlooked for the present; but in a given case it would be possible to observe some such marks as those indicated in Fig. 1. In the

specimen chosen there is a nearly central spot, the pith, around which numerous concentric lines—the "annual rings"—run. Radiating from the pith towards the periphery are cracks, the number, and length and breadth of which may vary according to the time the log has been exposed to the weather, and other circumstances; these cracks are due to the contraction of the wood as it "shrinks," and they coincide with medullary rays, as lines of weakness. Between these cracks are to be seen numerous very fine radiating lines indicating the course of the uninjured medullary rays, which again will vary in distinctness, &c., according to the species of timber.

This log of wood, with its annual rings and medullary rays, is clothed by a sort of jacket, consisting of cork and softer tissues, and termed the cortex, or, more popularly, the "bark" (an unfortunate word, which has caused much trouble in its time). The largest of the cracks is seen to traverse the whole radius of the face of the wood from centre to circumference, and also to pass through the cortex, which gapes widely.

The remaining cracks, however, stop short at a line which marks on the one hand the inner face of the cortex, and on the other the outer face of the wood: this line also represents the *cambium*, a thin sheet of

generative tissue which remains after giving rise to practically the whole of the wood (a very little in the centre excepted) and cortex visible in the woodcut. Since we are not concerned with the cortex and bark at present, it will be convenient to regard the log as "barked," and only deal with the wood or timber

FIG. 1.—A log of timber, showing radial cracks after lying exposed for some time. *a*, a large crack extending from pith to circumference; *b*, the cortex; *c*, medullary ray; *d*, cambium; *e*, annual ring; *f*, outer bark, proper. Reduced.

itself, in the condition to which the woodman reduces it after removing the cortex with certain implements.

If now we split such a log as Fig. 1 along the line of the big crack, neatly and smoothly, the well-known "grain" so often observed on planks of wood will come into view, and it will be noticed that the lines

which mark the "grain" are continuations of the lines which mark the annual rings, as shown in Fig. 2,

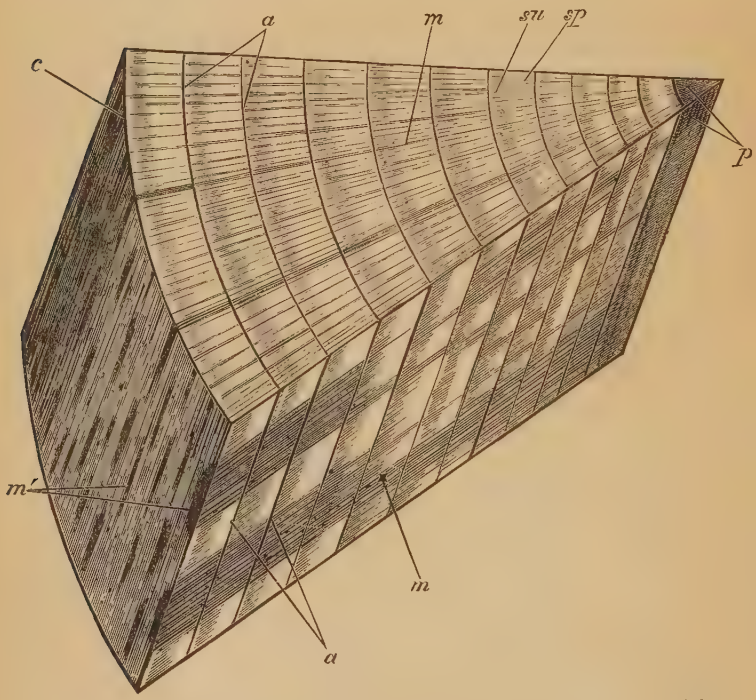

FIG. 2.—Portion of segment of wood from a log such as Fig. 1, supposed to be slightly magnified. *a*, annual ring; *m*, medullary rays; *m'*, the same in vertical section; *c*, the boundary line between one annual ring and another; *su*, autumn wood; *sp*, spring wood; *p*, the pith.

which represents on a larger scale a segment such as could be cut from a log in the way described. It is

clear from comparison of what has been said, and of the two figures, that the "annual rings" are simply the expression in cross-section of cylindrical sheets laid concentrically one over the other, the outermost one being that last formed. But on examining the medullary rays in such a piece of timber as that in Fig. 2, it will be noticed that they also are the expression of narrow radial vertical plates which run through the concentric sheets: the medullary rays are in fact arranged somewhat like the spokes of a paddle-wheel of an old type of steamer, only they differ in length, breadth, and depth, as seen by comparing the three faces of the figure. It is to be noticed that the medullary rays consist of a different kind of tissue from that which they traverse, a fact which can only be indicated in the figure by the depth of shading. It is also to be observed that the "annual rings" show differences in respect to their tissue, as marked by the darker shading near the boundary lines on the outer margin of each ring. In order to understand these points better, it is necessary to look at a piece of our block of timber somewhat more closely, and with the aid of some magnifying power. For the sake of simplicity it will be convenient to select first a piece of one of the timbers known as "deal" (firs, pines, &c.), and to observe it in the same direction as we

commenced with, *i.e.* to examine a so-called transverse section.

The microscope will show us a figure like that in the woodcut (Fig. 3). There are to be seen certain angular openings, which are the cross sections of the long elements technically called *tracheides*, shown in elevation in Fig. 4. It will be noticed that whereas along some parts of the section these openings are large, and as broad in one direction as in the other, in other parts of the section the openings are much smaller, and considerably elongated in one direction as compared with the other. The band of small openings naturally looks more crowded and therefore darker than the band of larger openings, and it is to this that the differences in the shading of the annual rings in Fig. 2 are due. But it is not simply in having larger lumina or openings that the dark band of tracheides is distinguished from the lighter one: the walls of the tracheides are often also relatively thicker, and obviously a cubic millimetre of such wood will be denser and contain more solid substance than a cubic millimetre of wood consisting only of the larger thin-walled tracheides. It is equally obvious that a large block of wood in which the proportion of these thick-walled tracheides with small lumina is greater (with reference to the bands of thin-walled tracheides)

will be closer-grained, and heavier, than an equal volume of the wood where the thin-walled tracheides with large lumina predominate.

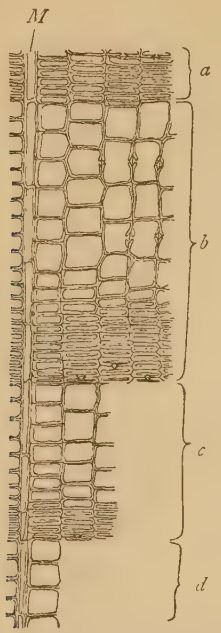

FIG. 3.—Portions of four annual rings from a thin transverse section of the wood of a Conifer, such as the spruce-fir. *M*, a medullary ray; *b* and *c* show the entire breadth of two annual rings; *a*, autumn wood of an annual ring internal to *b* (and therefore older than *b*); *d*, spring wood of an annual ring external to *c* (and therefore younger than *c*). Bordered pits are seen in section on some of the tracheides. Magnified about 100 times.

Returning now to the section (Fig. 3), it is to be observed that the differences in the zones just referred to enable us to distinguish the so-called "annual

rings." The generally accepted explanation of this is somewhat as follows. In the spring-time and early summer, the cambium-cells begin to divide, and those on the inner side of the cylinder of cambium gradually become converted into tracheides (excepting at a few points where the cells add to the medullary rays), and this change occurs at a time when there is (1) very little pressure exerted on the inner parts of the trunk by the cortex and corky bark, and (2) only comparatively feeble supplies are derived from the activity of the leaves and roots, in the still cool weather and short days with little sunlight. In the late summer, however, when the thickened mass of wood is compressed by the now tightened jacket of elastic bark which it has distended, and the long, hot bright sunny days are causing the numerous leaves and roots to supply abundance of nutriment to the growing cambium cells, it is not surprising that these cells cannot extend themselves so far in the radial direction (*i.e.* in a line towards the centre of the compressed stem), and that their walls are thickened by richer deposits of woody material supplied quickly to them.

As the winter approaches, the cambium ceases to be active, and it then remains dormant for several months. When its cells are awakened to renewed growth and division in the following spring, they at

once begin to form the tracheides with thin walls and large lumina, because the pressure previously exerted by the cortical jacket has been reduced by its cracking, &c. during the winter rest, and it is the sharp contrast thus displayed between the newly-formed tracheides with thin walls and large lumina, and the compressed denser ones of the previous summer on which they suddenly abut, that produces the impression of the "annual ring."

It is now time to attempt to give some clearer ideas of what this "cambium" is, and how its cells become developed into tracheides. But first it is necessary to point out that each tracheide examined singly, is a long, more or less tubular and prismatic body, with bluntly tapering ends, and the walls of which have certain peculiar markings and depressions on them, as seen in Fig. 4. We cannot here go into the important signification and functions of these markings and depressions however, since their study will need a section to themselves. It must suffice for the present to state that the markings have reference to the minute structure of the cell-walls, and the depressions are very beautiful and complicated pieces of apparatus to facilitate and direct the passage of water from the cavity of one tracheide to that of another. Now, the cambium is a thin cylindrical sheet of cells with very

delicate walls, each cell having the form of a rectangular prism with its ends sharpened off like the cutting edge of a carpenter's chisel: this prism is

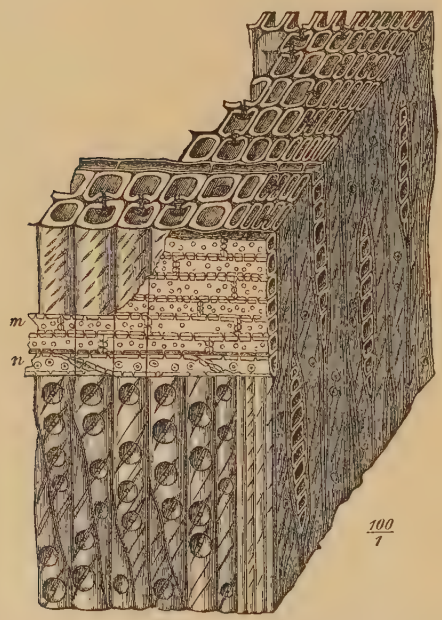

FIG. 4.—A small block of wood from a spruce-fir, supposed to be magnified about 100 times, showing elevation and sectional views of the tracheides of the autumn (to the right) and spring wood, and medullary rays (*m n*) running radially between the tracheides. (After Hartig.)

broader in the direction coinciding with the plane of the sheet of cambium—*i.e.* in the tangential direction, with reference to the trunk of the tree—than in the

direction of the radius of the stem; and the chisel-edge must be supposed to run in the direction parallel to that of a medullary ray, *i.e.* radially. From the first, each cambial cell contains protoplasm and a nucleus, and is capable of being nourished and of growing and dividing. It is only at or near the tips of the branches, &c., that these cambium-cells are growing much in length, however; and in the parts we are considering they may be for the most part regarded as growing only in the radial direction; more rarely, and to a slight extent, in the tangential direction also, as the circumference of the cylinder enlarges. After a cambial cell has extended the superficial area of its walls by growth in the radial direction to a certain amount, a septum or division wall arises in the longitudinal tangential plane, and two cells are thus formed in place of one: this process of division may then be repeated in each cell, and so the process goes on. This is not the place to lay stress on certain facts which show that a single layer of cells probably initiates the division: it suffices to point out that by the above process of division of the cambial cells there are formed radial rows of prismatic cells, as indicated in Fig. 5, where the arrow points along a radius towards the centre of the stem. It is true such radial rows of cells are also developed in smaller

numbers towards the outside of the cambium cylinder (*i.e.* to add to the cortex) but we are now only

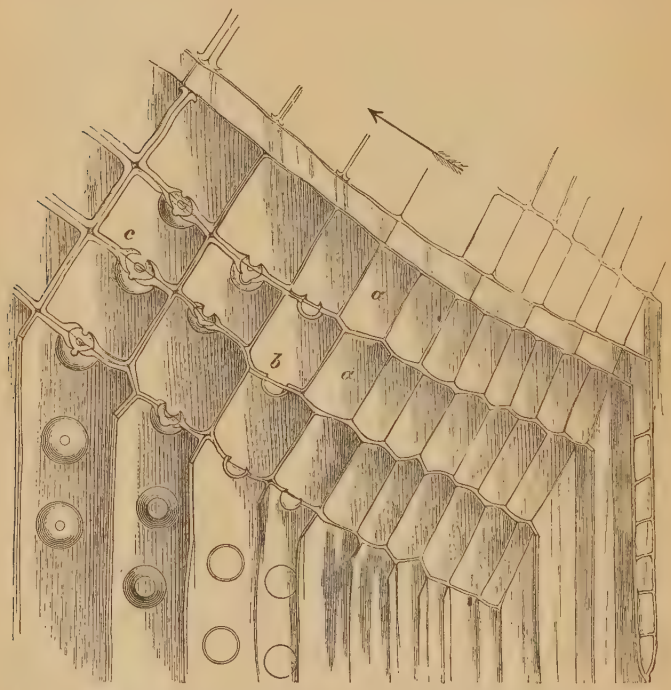

FIG. 5.—Portion of cambium of a fir, showing the development of the young wood tracheides from the cambium-cells. The arrow points to centre of the stem. The cambium-cells at length cease to divide, and the walls become thicker (*a*), except at certain areas, where the bordered pits are developed (*b* and *c*). To the right is a medullary ray. Highly magnified, and the contents of the cambium-cells omitted for clearness.

concerned with the wood, and therefore only regard those cells which are developed on the inside (*i.e.*

towards the centre of the stem). After a time the oldest of these cells (*i.e.* those nearest the centre of the stem) cease to divide, and undergo changes of another kind: the process of division is still going on in the younger ones, however; and so the radial rows are being extended by additions of cells at their outer ends. Of course, this is normally proceeding along the whole area of the cylindrical sheet of cambium, and therefore over the whole surface of the wood of the stem and roots, with their branches.

Confining our attention for the present to one of the innermost, oldest cells of the cambium, which has ceased dividing (*aa* in Fig. 5), we find that it enlarges somewhat in the radial direction, and then its hitherto very thin walls become thicker; in fact, the protoplasm in its interior absorbs food-materials, and changes them into a peculiar substance which it plasters or builds on to the inner sides of the cell-wall, so to speak, until the wall is rendered much thicker. This thickening process is withheld at certain places only—the thin depressions or "pits" already referred to. Two chief changes result now: (1) the whole of the living contents of the young wood-cell gradually become used up, and eventually disappear without leaving any trace, their place being occupied by water and air in most cases; and (2) the thickening substance

built on to the inside of the walls undergoes changes which convert it into true wood-substance—in botanical language, the walls become lignified. The cells *b* and *c* in Fig. 5 illustrate what is meant.

During all these changes, which occupy several or even many hours or days, according to circumstances, it will be observed that the definitive shape of the cell is gradually completed, and then alters very little: the prismatic cambium-cell has become a prismatic tracheide, with thicker, lignified walls, and containing air and water (with minute quantities of mineral substances dissolved in it) in place of protoplasm and nutritive substances. It is not necessary here to speak of other and more subtle changes which may eventually cause slight displacements, &c., of these cells.

If I have succeeded in making the chief points in this somewhat complicated process clear, there will be little difficulty in explaining what occurs in other parts of the cambium-cylinder. The cambium-cells which happen to stand in the same radial row as the cells of a medullary ray, simply go on being converted into cells of the medullary ray, instead of into tracheides; cells which differ from the tracheides chiefly in retaining their living contents and nutritive materials—*i.e.* substances like starch, proteids, sugars, &c., which are used as food by the plant. Again,

those cells of the cambium which are divided off on the outer side of the cylinder (they are always fewer in number) are gradually transformed into elements of the cortex, and many of them finally enter into the composition of the bark proper.

Now and again, but much more rarely, a radial row of cambial cells which, from their position, it would appear should be converted into tracheides of the wood, alter their destiny, so to speak, and become the originators of a new medullary ray. But I must pass over these and some other minor peculiarities, and refer to the illustrations for further details.

If now, instead of a log of deal, or coniferous wood, we direct attention to the timber of a dicotyledonous tree, such as the oak, ash, beech, chestnut, poplar, &c., the differences in detail will be found to be not very great in relation to the broad features here under consideration. Turning again to Fig. 1, it would be possible to select a cut log of any of these timbers which presented all the salient characters there exhibited. The "bark" would present external differences in detail—such as in roughness, colour, thickness, &c. —but it could still be described, as before, as a more or less corky jacket around the whole of the wood: the cut face would show the timber marked by more or less numerous and prominent "annual rings,"

traversed by smaller or larger medullary rays, radiating from the central pith, and passing across the cambium to the cortex. Moreover, cracks would be apt to form on exposure, as before; the opening occurring along the lines of medullary rays—lines of weakness.

Again, if we cut a segment of the wood, like Fig. 2, the chief features would present themselves as there shown, and the lines of demarcation indicating the annual rings would be found to be due to the sharp contrast between the spring wood and the autumn or summer wood, as before.

On closely examining a transvere section of such a piece of timber, however, we should find differences which at first sight appear profound, but which on reflection and comparison turn out to be of more relative significance, from the present point of view, than might be expected.

Selecting a given example, that of the beech for instance, the first difference which strikes us (Fig. 6) is a number of relatively very large openings on the transverse section: these are the vessels—pitted vessels—long tubular structures which are not formed by the cambium of the conifers. Each vessel may be regarded as a tube made by the joining of a long vertical row of tracheides, the lumina of which become

continuous as they pass out of the cambium stage. Between these vessels are much more numerous elements with very small lumina and thick walls: the latter are the wood-fibres proper, and have to be technically distinguished from the apparently somewhat similar wood-tracheides of the pines, firs, &c. Each fibre is, in effect, a tracheide with much thicker cell-walls than usual, and devoid of the characteristic "bordered pits" referred to when speaking of those structures: it is essentially a tough, strengthening element. Here and there, scattered in small groups, are certain rows of shorter cells, which, however, are not very numerous in the beech: they are called wood-parenchyma (Fig. 6, *wp.*), and occur particularly in the vicinity of the vessels. These wood-parenchyma cells are produced by the cambium-cell becoming divided across into several superposed short chambers, which retain their living contents: they resemble the cells of medullary rays in nearly all respects.

It is beside the purpose here to describe in detail the histology of the beech-wood, and reference may be made to the figures for further particulars. It may suffice to point out that all the elements—cells, fibres, and vessels—are formed as before by the gradual development of cambium cells; and the same is true,

generally, of the medullary rays here that is true of those of the pines and firs, &c.

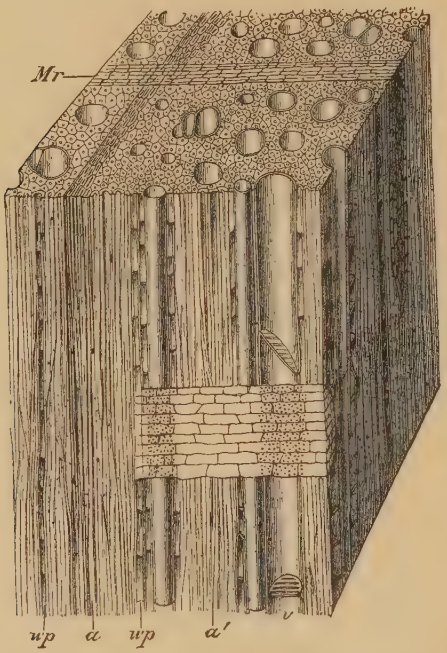

FIG. 6.—A piece of wood from a dicotyledonous tree (beech), supposed to be magnified about 100 times. *Mr*, a medullary ray running across the transverse section: the dark band crossed by this ray is the autumn wood (*a*), formed of closely-crowded wood-fibres and tracheides: *v*, a large vessel in section: others are seen also—they are smaller and fewer towards the autumn wood; *a'*, wood-fibres, of which most of the timber is composed; *wp*, wood-parenchyma cells.

Attention is to be directed to the fact, which is here again evident, that the line of demarcation between

any two "annual rings" is due to the sudden apposition of non-compressed elements upon closely-packed and apparently compressed elements: the latter were formed in the late summer, the former in the spring. Moreover, the spring wood usually contains more numerous vessels, with larger lumina than the autumn wood, and for the same reasons as before: in this particular case, again, the fibres of the autumn wood are darker in colour. It should be stated, however, that many dicotyledonous trees show these peculiarities more clearly than the beech: others, again, show them less clearly.

Now it is obvious that, other things being equal, the spring wood, with its more numerous and larger vessels, and its looser tissue generally, will yield more readily to lateral pressures and strains than the denser autumn wood; and the like is true of the pines and firs—the closely-packed, thick-walled tracheides of the autumn wood furnish a firmer and more resistant material than the larger, thinner-walled tracheides of the spring wood. To this point we shall have to return presently.

CHAPTER II.

TIMBER, ITS PROPERTIES AND VARIETIES.

THE enormous variety presented by the hundreds of different kinds of woods known or used in different countries depends for the most part on such peculiarities as I have referred to above, together with some others which have not as yet been touched upon. Everybody knows something of the multitudinous uses to which timber is put, and a little reflection will show that these uses are dependent upon certain general properties of the timber. Speaking broadly, the chief properties are its weight, hardness, elasticity, cohesion, and power of resisting strains, &c., in various directions, its durability in air and in water, and so forth; moreover, special uses demand special properties of other kinds also, and the colour, closeness of texture, capacity for receiving polish, &c., come into consideration.

Now, there is no doubt that the structure of the wood as formed by the cambium is the chief factor in deciding these technological characters: it is not the only factor, but it is the most important one. Consequently no surprise can be felt that those who are interested in timber have of late years turned their attention to this subject with a view to ascertain as much as possible about this structure, and to see whether it can be controlled or modified, what dangers it is subject to, and how far a classification of timbers can be arrived at. The more the subject is studied, the more interesting and practically important the matter becomes. The results already obtained (though the study is as yet only in its infancy) have thrown light on several burning questions of physiology—as witness the researches of Sachs, Hartig, Elfving, and Godlewski, on that old puzzle, to account for the ascent of water in tall trees. The study is, moreover, of first importance for the comprehension of the destruction of timber, due to "dry-rot" and the parasites which cause diseases in standing trees, as is shown by the brilliant researches of Prof. R. Hartig on the destruction of timber by Hymenomycetes; and again as yielding trustworthy information as to the value of different kinds of timber in the arts, and enabling us to recognize foreign or new woods

of value. In support of this statement it is only necessary to call attention to the "Manual of Indian Timbers," prepared for the Indian Government by Mr. Gamble; or to refer to the beautiful series of wood-sections prepared by Nördlinger.

It is, of course, impossible in a small book like this to do more than touch upon a few of the more interesting points in this connection; but I may shortly summarize one or two of the more striking of these peculiarities of timbers, if only to show how well worth further investigation the matter is.

Many timbers, from both tropical and temperate climates, exhibit the so-called "annual rings" on the transverse section; but this is not the case with all. Most European timbers, for instance, are clearly composed of such layers; but in some cases the layers ("rings" on the transverse section) are so narrow and numerous that the unaided eye can scarcely distinguish them, or the differences between the spring and autumn wood are so indistinctly marked that they may appear to be absent, or are at least obscure, as in the olive, holly, and orange, for instance. It is in the tropics, however, that timber without annual rings is most common, possibly because the seasons of growth are not sufficiently separated by periods of rest to cause the formation of sharply-

marked zones, corresponding to spring and autumn wood, *e.g.* some Indian Leguminosæ, &c. Zones of tissue of other kinds (especially wood-parenchyma) often occur in such timbers, and have to be under-

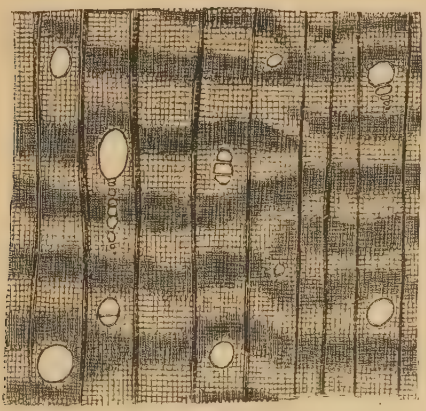

FIG. 7.—Transverse section of the wood of *Pongamia glabra*, Vent, selected to show a type of timber not uncommon in India. No distinct annual rings appear, but the wood is traversed by wavy bands of tissue, which may run into one another or not. The vessels ("pores") are few and scattered, and differ in size; the medullary rays well marked, but not large. To this type—differing in other details—belong many species of figs, acacias and other Asiatic Leguminoseæ, &c.

stood, since they affect the property of the wood very differently, *e.g.* some of the figs.

None of the conifers or dicotyledonous trees, however, are devoid of medullary rays, and distinctive characters are based on the breadth and numbers of these: as examples for contrast may be cited the fine

rays of the pines and firs, and the coarse obvious ones of the oaks.

Again, the prominence or minuteness, or even (Coniferæ and a few Magnoliaceæ) absence, of vessels in the secondary wood afford characters for classification.

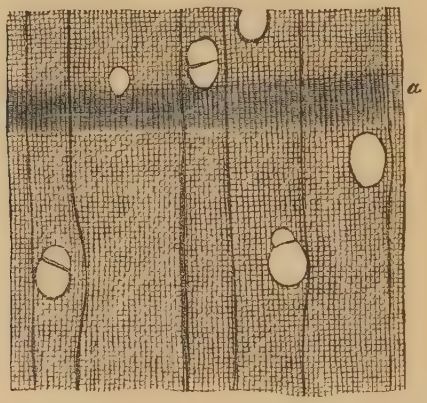

FIG. 8.—Transverse section of wood of *Tamarindus indica*, Linn., selected to show a not uncommon type of Asiatic timber. The annual rings are indistinct, but occasionally indicated by denser tissue (*a*). The vessels are fairly large and few, and scattered much as in Fig. 7, but there are no such broad bands of cells as there.

The contrast between the extremely small vessels of the box and the very large ones of some oaks and the chestnut, for instance, is too striking to be overlooked. Then, again, in some timbers the vessels are distributed more or less equably throughout the

"annual ring," as in the alder, some willows and poplars, &c.; whereas in the chestnut and others they are especially grouped at the inner side of the annual zone (*i.e.* in the spring wood), and in some cases these groupings are such as to form characteristic figures on the transverse section, as in some oaks, *Rhamnus*, &c.

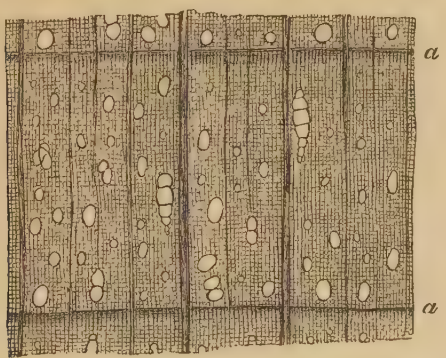

FIG. 9.—Transverse section of the wood of *Acer pseudo-platanus*, selected to show a type of timber common in Europe. The annual rings (*a*) are well-marked and regular. The vessels are small and numerous, and scattered somewhat equally over the whole breadth of the ring. The medullary rays are numerous, some broad, some fine. Many European timbers (beech, hornbeam, lime, &c.) agree with this type, except in detail.

In the woodcuts (Figs. 7-10) I have given four examples illustrating a few of the chief points here adverted to.

Passing over peculiar appearances due to the distribution of the wood-parenchyma between the

vessels, as exemplified by the figs and the maples, as well as minor but conspicuous features which enable experts to recognise the timber of certain

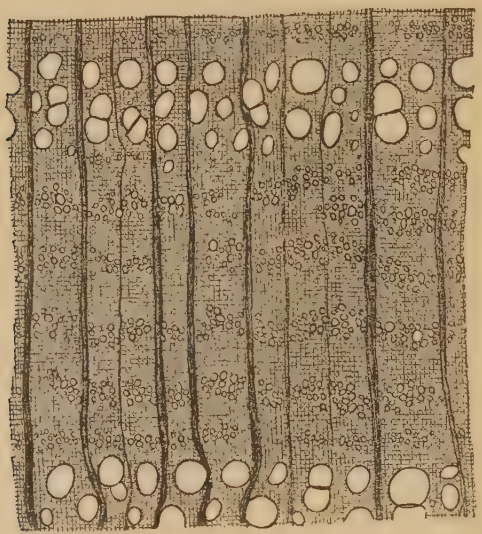

FIG. 10.—The transverse section of wood of the common elm (*Ulmus campestris*), selected as a common type of European timber. The annual rings are very distinct, owing to the large vessels in the spring wood; the vessels formed during the summer and autumn are grouped in bands or zones. The medullary rays are numerous, but not very broad. The oak, ash, chestnut, and others agree in the main with this type, differing chiefly in the *mode of grouping* of the smaller vessels, and in the *breadth* of the medullary rays.

trees almost at a glance, I now proceed to indicate a few other peculiarities which distinguish different timbers.

The weight of equal volumes of different woods differs more than is commonly supposed, and there are certain details to be considered in employing weight as a criterion which have not always been sufficiently kept in mind.

A cubic foot of "seasoned" timber of the Indian tree *Hardwickia binata* weighs about 80 lbs. to 84 lbs., while a cubic foot of *Bombax malabaricum* may weigh less than 20 lbs., and all gradations are possible with various timbers between these or even greater extremes. If we keep in mind the structure of wood, it is evident that the weights of equal volumes of merely seasoned timber will yield only approximate results. For even if the seasoning, weighing, &c., are effected in a constant atmosphere, woods which differ in "porosity" and other properties will differ in the extent to which they absorb moisture from damp air or give it up to dry air.

In our climate, timber which is felled in April or May, generally speaking, contains much more water than if felled in July and August: it is, in fact, no uncommon event to find that about half the weight, or even more, of a piece of recently felled timber is due to the water it contains. If this water is driven off by heat, and the piece of wood thoroughly dried, the latter will be found to weigh so much less, but it

will gradually increase in weight again as it imbibes moisture.

Now it happens that the weight of a piece of timber, compared with that of an equal volume of some standard substance—in other words, the so-called specific weight—is of very great importance, because several other properties of wood stand in relation with it, *e.g.* the hardness, durability, value as fuel, tendency to shrink, &c. Fresh-cut timber in very many cases contains on an average about 45 to 50 per cent. of its weight of water, and if "seasoned" in the ordinary way this is reduced to about 15 to 20 per cent.; but the fresh timber also contains air, as may easily be shown by warming one end of a piece of fresh wood at the fire or in hot water and watching the bubbles driven out, and the seasoned timber contains less water and more air in proportion, so that we see how many sources of error are possible in the usual weighings of timber. At the same time, many comparative weighings of equal volumes of well-seasoned timber do yield results which are of rough practical use.

The fact is that the so-called "specific weight" of timber, as usually given, is not the specific gravity of the wood-substance, but of the *plus* entangled air and water. It is interesting to note that, although we associate the property of floating with wood, timber

deprived of its air will sink rapidly, being about half as heavy again as water, volume for volume.

The point just now, however, is not to discuss these matters in detail, but rather to indicate that, other things equal, the density of a piece of timber will be greater, the more of that closely-packed, thick-walled autumn wood it contains ; while the timber will be specifically lighter and contain more air when dry, the greater the proportion of the looser, thin-walled spring wood in its "annual rings." In other words, if we could induce the cambium to form more autumn wood and less spring wood in each annual ring, we could improve the quality of the timber ; and, in view of the statement which has been made, to the effect that large quantities of timber of poor quality reach the Continental wood-yards every year, this is obviously an important question, or at any rate may become one. The remainder of this chapter must be devoted to this question alone, though it should be mentioned that several other questions of scientific and practical importance are connected with it.

The first point to notice is that the cambium-cells, like all other living cells which grow and divide, are sensitive to the action of the environment. If the temperature is too high or too low, their activity is affected and may even be brought to an end ; if the

supply of oxygen is too small, their life must cease, since they need oxygen for respiration just as do other living cells; if they are deprived of water, they cannot grow—and if they cease to grow they cannot divide, and any shortcomings in the matter of water-supply will have for effect a diminution of activity on the part of the cambium. The same is true of the supply of food-substances; certain mineral salts brought up from the soil through the roots, and certain organic substances (especially proteids and carbo-hydrates) prepared in the leaves, are as necessary to the life of a cambium-cell as they are to the life of other cells in the plant. Now, since the manufacture of these organic substances depends on the exposure of the green leaves to the light, in an atmosphere containing small quantities of carbon-dioxide, and since the quantities manufactured are in direct relation to the area of the leaf-surface—the size and numbers of the leaves—it is obvious that the proper nourishment of the cambium is directly dependent on the development of the crown of foliage in a tree. Again, since the amount of water (and mineral salts dissolved in it) will vary with the larger or smaller area of the rootlets and absorbing root-hairs (other things equal), this also becomes a factor directly affecting our problem. Of the inter-dependencies of other kinds between these various

factors we cannot here speak, since they would carry the argument too far for the space at command ; some of them are obvious, but there are correlations of a subtle and complex nature also.

First as to temperature. The dormant condition of the cambium in our European winter is directly dependent on the low temperature : as the sun's rays warm the environment, the cambium cells begin to grow and divide again. The solar heat acts in two ways : it warms the soil and air, and it warms the plant. Wood, however, is a bad conductor of heat, and the trunk of the tree is covered by the thick corky bark, also an extremely bad conductor, and it would probably need the greater part of the early summer to raise the temperature of the cambium sufficiently for activity in the lower parts of a tree by direct solar heat : the small twigs, on the contrary, which are covered by only a thin layer of cortex, and epidermis, are no doubt thus warmed fairly rapidly, and their early awakening is to be referred to this cause. The cambium in the trunk, however, is not raised to the requisite temperature until the water passing up through the wood from the roots is sufficiently warm to transmit some of the heat brought with it from the soil to the cells of the cambium. This also is a somewhat slow process, for it takes some time for the

sun's rays to raise the temperature of the soil while the days are short and the nights cold. It has been shown that the cambium in the lower part of the trunk of a tree may be still dormant three weeks or a month after it has begun to act in the twigs and small branches; and it has also been pointed out that trees standing in open sunny situations begin to renew their growth earlier than trees of the same species growing in shady or crowded plantations, where the moss and leaf-mould, &c., prevent the sun from warming the soil and roots so quickly. These observations have also a direct bearing on the later renewal of cambial activity in trees growing on mountains or in high latitudes. Moreover, though I cannot here open up this interesting subject in detail, these facts have their connection with the dying off of temperate trees in the tropics, as well as with the killing of trees by frost in climates like our own. One important practical point in this connection may be adverted to. Growers of conifers are well aware that certain species cannot be safely grown in this country (or only in favoured spots) because the sun's rays rouse them to activity at a time when spring frosts are still common at night, and their young tissues are destroyed by the frosts. Prof. R. Hartig has pointed out a very instructive case. The larch is an Alpine

plant, growing naturally at elevations where the temperature of the soil is not high enough to communicate the necessary stimulus to the cambium until the end of May or June. Larches growing in the lowlands, however, are apt to begin their renewed growth in April, and frosted stems are a common result, a point which (as the botanist just referred to also showed) has an important bearing on that vexed question—the "larch-disease."

The supply of oxygen to the cambium is chiefly dependent on the supply of water from the roots, and the aëration of the stem generally. The water begins to ascend only when the soil is warm enough to enable the root-hairs to act, and new ones to be developed, and the supply of mineral salts goes hand in hand with that of water.

Now comes in the question of the sources of the organic substances. There is no doubt that the cambium at first takes its supply of food-materials from the stores which have been laid by, in the medullary rays and wood-parenchyma, &c., at the conclusion of the preceding year; and it is known that special arrangements exist in the wood and cortex to provide for this when the water and oxygen arrive at the seat of activity.

Assuming that all the conditions referred to are

favourable, the cambium cells become filled with water in which the necessary substances are dissolved, and distended (become turgid, or turgescent, as it is technically called) sufficient for growth. Speaking generally, and with reference chiefly to the trunk of the tree, which yields the timber, the distension of the cells is followed by growth in the direction of a radius of the stem, and division follows in the vertical plane, tangential to the stem. Then the processes already described in connection with Fig. 5 repeat themselves, and the trunk of the tree grows in thickness.

Now it is obvious that the thickening of the mass of timber inside the cylinder of cambium must exert pressure on the cortex and bark—must distend them elastically, in fact—and some ingenious experiments have been made by De Vries and others to show that this pressure has an effect in modifying the radial diameter of the cells and vessels formed by the cambium. Several observers have promulgated or accepted the view that the differences between so-called spring and autumn wood are due to the variations in pressure of the cortex on the cambium, but the view has lately gained ground, based on experimental evidence, that these differences are matters of nutrition, and a recent investigator has declared that the thick-walled elements and small

sparse vessels characteristic of autumn wood can be produced, so to speak, at will, by altering the conditions of nutrition.

It is authoritatively stated that the pines of the cold northern countries are preferred for ships' masts in Europe, and that the wood-cutters and turners of Germany prize especially the timber of firs grown at high elevations in the Bavarian Alps. Now the most striking peculiarity of the timbers referred to is the even quality of the wood throughout: the annual rings are close, and show less of the sharp contrast between thin-walled spring wood and thick-walled autumn wood, and it has been suggested that this is due to the conditions of their nutrition, and in the following way. The trees at high elevations have their cambium lying dormant for a longer period, and the thickening process does not begin in the lower parts of the trunk until the days are rapidly lengthening and the sun's rays gaining more and more power: the consequence is that the spring is already drawing to a close when the cambium-cells begin to grow and divide, and hence they perform their functions vigorously from the first.

One of the most interesting experiments in this connection came under my observation during the summer of 1887. There is a plantation of larches at

Freising near Münich, with young beeches growing under the shade of the larches. The latter are seventy years old, and are excellent trees in every way. About twenty years ago these larches were deteriorating seriously, and were subsequently "under-planted" with beech, as foresters say—*i.e.* beech-plants were introduced under the shade of the larches. The recovery of the latter is remarkable, and dates from the period when the under-planting was made.

The explanation is based on the observation that the fallen beech-leaves keep the soil covered, and protect it from being warmed too early in the spring by the heat of the sun's rays. This delays the spring growth of the larches: their cambium is not awakened into renewed activity until three weeks or a month later than was previously the case, and hence they are not severely tried by the spring frosts, and the cambium is vigorously and continuously active from the first.

But this is not all. The timber is much improved: the annual rings contain a smaller proportion of soft, light spring wood, and more of the desirable summer and autumn wood consisting of closely-packed, thick-walled elements. The explanation of this is that the spring growth is delayed until the

weather and soil are warmer, and the young leaves in full activity; whence the cambium is better nourished from the first, and forms better tracheides throughout its whole active period. Such a result in itself is sufficient to repay the investigations of the botanist into the conditions which rule the formation of timber, but this is by no means the only outcome of researches such as those carried on so assiduously by Prof. Hartig in Münich, and by other vegetable physiologists.

It is easy to understand that the toughness, elasticity, and such like qualities of a piece of timber, depend on the character of the tracheides, fibres, &c., of which it is chiefly composed. Investigations are showing that the length of such fibres differs in different parts of the tree. Sanio has already demonstrated that in the Scotch pine, for instance, the tracheides differ in length at different heights in the same trunk, becoming longer as we ascend, and also are longer in the outer annual rings than in the inner ones as the tree grows older, up to a certain period; and this is in accordance with other statements to the general effect that for many years the wood improves, and that better wood is found at the base of the trunk.

However, it is impossible to pursue these subjects

in all their details: my object is served by showing how well worthy of the necessary scientific study is timber even to those who are only concerned with it in its usual conditions, and within those limits of variation in structure and function which constitute health. The importance of the subject in connection with the modern development of biology along the grand road of comparative physiology, does not need insisting upon here. It will be the object of further chapters to show how it is, if possible, still more important and interesting to know the structure and functions of healthy timber, before the practical man can understand the diseases to which timber is subject. At the same time it must be clearly borne in mind that these are but sketches of the subject; for it is as true of trees and their diseases as it is of men and human diseases, if you would be trainers and doctors you must know thoroughly the structures and peculiarities of the beings which are to be under your care.

CHAPTER III.

THE CLASSIFICATION OF TIMBERS.

THE problem of how to arrange the various kinds of timbers so that they may be easily recognised, has occupied the attention of many people for a long time, but it must be confessed that none of the proposed methods has resulted in a satisfactory classification, and it may be doubted whether all the difficulties are likely to be surmounted: nevertheless much may be done towards system, and the principles employed are not only interesting in themselves, but are also worth examination as showing how numerous facts about timber may be collated, and compared and contrasted. In any case, while allowing that it is as yet impossible so to arrange a collection of pieces of timber that all the kinds can be recognised at a glance, it must be admitted that the attempt to do so at least aids one in determining many kinds of wood by means of their

peculiar characters: of course more can be done by taking into consideration other characters in addition, such as those of the bark, buds, leaves, &c.—but we then approach the methods employed in the classification of plants in the natural system of botanists. The object under consideration is to arrange small pieces of wood alone, so that, by characters peculiar to each, the expert (for of course it needs practice and experience) can recognise them.

Like all systems of classification, that of timbers offers every degree of difficulty, and it is easy and natural to begin with cases which present well-marked and readily recognisable features. Excluding such "woods" as those of the tree-ferns, palms, Cycads, and others which do not properly constitute "timber," I shall direct attention only to the Conifers and Dicotyledons, and among these, while regarding especially the true timber-trees, I propose to give a summary of the chief features which prove useful in classifying them. This of course places out of consideration any scheme (such as those adopted by the late Professor De Bary, and others) for the classification of fibro-vascular bundles —the bi-collateral bundles of Cucurbitaceæ, &c.; the radial ones of most roots; closed, as contrasted with open collateral bundles, &c.—all these matters

are foreign to our purpose, and will not help us in classifying timbers properly so called.

There are, however, a few accessory phenomena which prove useful occasionally, if pieces of timber are obtained which include these.

For instance the pith, though of course not belonging to the wood, sometimes presents marked features, worth noting because it is occasionally included in the block of timber examined, or can be obtained. Thus, the pith on transverse section is pentagonal or rayed in *Quercus* (oaks) and a few other plants, while it is chambered in *Juglans* (walnut): usually small and insignificant, it is relatively abundant in *Sambucus* (elder) and *Ailanthus*.

Another of these accessory characters, as we may term them, is obtained by comparing the inner and older wood of the tree with the outer, younger wood, and it should be remarked in passing that much trouble is sometimes caused by the selection of timber-specimens which do not show these characters. Very many woods, as is well known, exhibit marked peculiarities in their inner or "heart-wood"—the *duramen* of botanists—which is harder, or heavier, or of some decided colour, and constitutes a true "heart-wood," as contrasted with the softer, lighter, non-coloured "sap-wood" (*alburnum*): in other cases no

obvious differences are to be noticed, and the tree is said to have no "heart," but to consist entirely of "sap-wood. I will not stop to discuss the physiological significance of these cases, but simply quote, as examples of woods that can be distinguished almost by their "heart-wood" alone, Ebony, where it is black, *Guaiacum* (green), *Cæsalpinia Sappan* (red), Logwood (purple), and numerous instances suggest themselves where the characters of the "heart-wood" are useful.

Yet another accessory feature is the occurrence of certain peculiar discoloured spots or patches in certain woods, which are always suggestive and sometimes distinctive: these are known as "medullary spots" or "pith flecks," and usually look like small patches of rust in the substance of the wood. They are not at all uncommon, and may be seen in the birches, hawthorn, species of *Pyrus*, *Salix*, &c.: their nature needs further investigation, but we are only concerned here with the fact of their occurrence.

In a certain sense we must regard the resin-canals of some pines, firs, &c., and some *Anacardiaceæ*, as useful accessory characters: many Conifers especially being distinguished by their presence. These resin-canals have nothing to do with the true vessels of the wood of Dicotyledons, of which more will be said presently

Turning our attention now to those features which are more generally characteristic of timbers, it has to be admitted that their employment is a matter of considerable difficulty in some cases, though it is easy enough in others. I will describe some of the principal varieties as we proceed, and give a few illustrations in each case.

All Conifers and Dicotyledons which form timber are provided with medullary rays, and it has been found possible to make something of the variations they present in different cases. Thus, the medullary rays may be few and relatively far apart, as in *Laburnum* and *Robinia* (with 19 or 20 in a breadth of 5 mm.), or numerous and crowded, as in the oak (with 64 in a breadth of 5 mm.). *Rhododendron maximum* has as many as 140 in the same area, according to Nördlinger. Then, they may be very narrow, requiring at least a lens for their observation, as in the pines, ebony, horse-chestnut, willows, &c.; or sufficiently broad to be seen at a glance with the unaided eye, as in the oaks and *Casuarina*. All degrees of breadth from less than 0·005 mm. to 1 mm. occur, and the attempt has been made to cast them into six groups, or degrees of fineness, but it seems impossible to define all these groups: nevertheless we can speak of fine, medium, and broad rays

respectively, the common holly giving us a fairly medium breadth.

In some cases, and markedly so in the oaks, there are two kinds of medullary rays: large broad obvious ones, with more numerous finer ones between them. Such rays may also be distinguished as consisting of many or one series of cells—*pluri-seriate* and *uni-seriate* medullary rays. In some Conifers a resin-canal often occurs in the medullary ray: in the beech the broad rays widen out where they cross the boundary between the annual rings: in the hornbeam the so-called broad medullary rays are composed of several rays running parallel and close together.

The next general character I have to consider is that afforded by the presence or absence, &c. of the so-called "annual rings." It may be, and has been questioned whether zones indicating periodic changes in increment are ever absent from the timber of trees, but be this as it may there are certainly cases of tropical timbers where no such annual-rings, as they are called, can be distinguished by the unaided eye, or even with a lens: such timbers are said to be devoid of "annual rings." I say "so-called annual rings," because we are not yet sure that the periodic zones correspond in all cases with *annual* increment, though that is no doubt normally the case with all European

trees. Examples of timbers which show no annual rings on the transverse section are common among Indian timbers, *e.g.* iron wood, mango, ebony, &c. In the vast majority of common timbers, however, including many tropical forms, the transverse section always shows more or less concentric zones or rings: in many cases, as in oak, ash, teak, toon, &c., these are obviously the "annual rings," but in other cases, as in the figs, *Casuarina*, *Pongamia*, &c. the apparent rings are found to be of a different character, and due to concentric or excentric partial or complete zones of soft tissues, especially wood-parenchyma. I shall term these "false rings:" a little practice will enable the student to recognise them in most cases. It may be noted that in *Calophyllum*, and many *Sapotaceæ* and *Anonaceæ*, and others, these partial zones are made up of wavy, pale, bar-like markings between the medullary rays.

As to the timbers with undoubted rings, two chief types may be readily distinguished if the student understands the meaning of the line of demarcation between the annual rings.

In the one type the vessels in the spring-wood are so large or so numerous (or both), as contrasted with those in the autumn-wood of the same annual ring, that the boundary between any two rings is par-

ticularly sharp, owing to the contrast between the porous and the dense wood, *e.g.* oak, ash, plum, teak, &c. In the other of these chief types the line of demarcation is due to similar differences in the density of the fibrous and other elements of the wood rather than to contrast between porous (*i.e.* very vascular) and dense wood; the autumn-wood has very thick walls and small lumina, the spring-wood thinner walls and larger lumina, without special reference to the vessels, which are usually small and nearly evenly dispersed through the whole. As examples I may refer to the wood of birch, maple, horse-chestnut, *Shorea robusta*, &c. That difficulties in deciding must occur in some cases is only too evident, and it is well known that in individual cases departures from the type are produced by local disturbances—*e.g.* the formation of two so-called "annual rings" in one year, and (at least it is suspected and needs investigation) the suppression of the demarcation lines by changes due to climatic and other local influences. Nevertheless the characters usually work well in practice. It should be remarked that whereas the course of the annual rings is normally concentric and regular, it is wavy in some cases, *e.g.* barberry, where the crests of the waves project outwards at the medullary rays, whereas they project inwards in *Kalmia latifolia*, hornbeam, beech, &c.

The false zones of soft tissue are often seen to run into one another, whereas this is not the case with true rings, however excentric they are.

The next character of general importance is the presence or absence of vessels—often called "pores" by technologists—as seen on the transverse section; and there are certain peculiarities connected with them.

The first thing to note is a possible danger of the tyro mistaking the resin-canals of Conifers for these vessels of the wood: practical aquaintance with the irregular outline and very different structure and distribution of these canals will alone serve the student here. Vessels (excluding the small spiral vessels of the *proto-xylem* which form the so-called "medullary-sheath," and which do not come into consideration) are found in the wood of all Dicotyledons, except *Drimys* and one or two of its allies, while they are as regularly absent from that of the Conifers; consequently it is easy at the outset to distinguish the woods of these two great groups at a glance, at least with the aid of a lens. In the Dicotyledons, however, considerable differences are to be observed regarding the vessels; and first, as to their size.

The rule is that the vessels are largest and most numerous in the spring-wood, diminishing outwards

(in *Kalmia*, strange to say, the reverse is the case), as well seen in oak ; but in some cases the differences are so slight that we say the vessels are equal all over, *e.g.* box, birch, willow, alder, &c. The diameter of the vessels varies much in different cases, and very large ones may coexist with very small ones. Neglecting the wood of some climbers, where the vessels are easily seen with the unaided eye, and may be more than half a millimetre in diameter, we find examples of large vessels in the oak, ash, chestnut, walnut, &c., where they are visible without a lens, and of extremely small ones in box, birch, willow, maple, horse-chestnut, &c. All sizes between these extremes are to be met with, and Nördlinger has tried to arrange them in six groups, but I cannot recommend this, as it seems impossible to maintain them. The laburnum and the plane afford examples of medium-sized vessels.

Characters have been obtained from the mode of grouping of the vessels, or "pores," on the transverse section. Thus we have seen how their equal distribution, or concentration in the spring-wood, as the case may be, affects the classification as regards annual rings ; but besides this we find peculiarities of other kinds which are characteristic. In the hornbeam, for instance, there are long, sinuous lines of pores radiat-

ing between the medullary rays from centre to circumference of the stem. In other cases sinuous bands of small pores are seen running peripherally, and almost simulating false rings, *e.g.* the elm. Beautifully-arranged tongue-like or flame-like groups of pores are seen in the oaks, chestnut, *Rhamnus*, *Ulex*, &c., and these are very characteristic.

Attempts have been made to carry the examination of these features further by means of the microscope, and to distinguish woods where the pores are single from those where they are apt to be grouped in pairs, threes and fours, and so on ; but although it is true that the vessels are usually single in the box, for instance, and often in groups of five to twelve or more in holly and hazel, while less than twenty to fifty together rarely occur in *Rhamnus catharticus*, &c., I cannot find that the characters are either sufficiently constant or sufficiently obvious for practical purposes.

These, then, are the principal general characters which can be employed in classifying timbers, and we may now ask whether any others exist that could be made use of. The reply is that several others could be used more than they are if we had good records and scales of comparison. Some of these may be shortly indicated as follows: The *hardness* of different timbers may be very different. Thus the Indian *Bombax*

malabaricum is so soft that a pin may be easily driven into it, whereas *Mesua ferrea* is so hard that it turns the edge of almost any tool; between these extremes we find all degrees of hardness, and it is the moderately hard woods which are so useful for general purposes, *e.g.* teak and oak. The dry *weight* of a timber is usually not far out of proportion to its hardness, and characters can sometimes be derived from a sort of rough scale of weight—the weight of a cubic foot or metre, or some other unit being chosen for comparison. Thus, the wood of *Erythrina suberosa* may weigh as little as 13 lbs. the cubic foot, while that of *Hardwickia binata* may reach 84 to 85 lbs., and all degrees of heaviness are found in different timbers between such extremes. At the same time more information is needed as to the relative weights of equal volumes of wood, as we have already seen how fallacious ordinary rough-and-ready weighings may be, made, as they usually are, without any guarantee that each specimen was dried to the same extent: on the whole, we may, perhaps, call any timber light which, when air dry, weighs less than 30 lbs. per cubic foot, and moderately heavy if it reaches 40 to 50 lbs.; anything over 60 lbs. is decidedly heavy. The "closeness" or "porosity" of different timbers bears an obvious relationship to their hardness and

weight in most cases. Woods are also even-grained, or cross-grained, open, rough, &c., in various degrees.

The *colour* of a timber is sometimes a useful character, and has been already referred to when speaking of the heart-wood and sap-wood, which usually have different hues.

There are a few other characteristics afforded by special kinds of timber which should be noticed, though they cannot be made use of in a general classification. I refer particularly to such peculiarities as the *odours* of sandal-wood, deal, teak, toon, and the Australian pencil-cedar (*Synoum glandulosum*), &c. Certain special markings, such as the satiny lustre of satin-wood; the white mineral substances (apatite!) in the vessels of teak; the appearance of the polished surface, and a number of other features which come under the notice of the timber merchant and technologist must be passed over here, useful as they are for the recognition of special timbers on the spot.

A high authority has written, with respect to this subject, "It is not always easy to give in words an explanation of the reasons which lead one who is tolerably conversant with the structure of woods to pronounce an opinion; there are often characters of appearance, touch, colour, odour, &c., which afford

clues, as well as the arrangement and relative size of the pores and medullary rays, and the presence or absence of annual rings; so that it is really only experience and habit that can teach us to recognize, from a mere inspection of a wood, the place which it ought to occupy in the natural system." But while we may readily admit the general truth of this remark, it seems a just rejoinder that in so far as the characters of wood are capable of accurate description, it will become more and more possible to explain why the expert can recognise a piece of timber. Definiteness and system are the two things to aim at.

In order to illustrate the sort of lines along which a systematic tabulation of the characters of timber might be looked for, I subjoin a scheme of classification of some of the most important European and Indian timbers, and I may perhaps add my conviction that if observers will only continue to note peculiarities, and compare them in some such manner as this, it should be possible to obtain a much more complete classification than we could bring together now.

For the foresters' purposes in any country, many extremely valuable characters are to be obtained incidentally, as it were, to those of the timber proper, from observing the size of the tree, or shrub, or if

it is a climbing plant which yields the wood in question. Again, the bark and cortex in the young and older states—its colour, thickness, texture, mode of stripping, &c. Some trees are evergreen, others deciduous; some grow in swamps, others on dry plains or hills; some are gregarious, and so on. Moreover, in classifying the trees of a large country, the facts of geographical distribution of some of them can often be utilized—for instance, no one need look for teak on the Himalayan heights, nor for deodar in the plains of Southern India, and, again, *Heritiera littoralis* is a tree of the tidal forests of India and Burma, and is not likely to be seen by a forest-officer working away from such districts. Such facts as these, amplified and accurately generalized, might be made much use of in drawing up lists, &c., for the guidance of those at work in geographically different districts, as it is the timbers as commonly met with in the yards that need classifying.

It will be understood that the following table is of course intended to be, not a complete classification of timbers, but an illustration how such classification might be possible, and gradually improved as time and knowledge progress.

I. Conifers.

The wood (except immediately around the pith) contains no true vessels, though resin-canals occur in many cases in the autumn wood. Annual rings nearly always sharply marked, from the denser autumn zone. Medullary rays very fine and numerous.

A. There are no resin-canals in the wood.
   (1) No true "heart" is to be distinguished:
   e.g. Silver Fir; *Abies Webbiana.*
   (2) There is a distinct central "heart-wood":
   e.g. Yew, Juniper, Deodar; *Wellingtonia.*

B. Resin-canals are present, at least in the autumn-wood.
   (3) No true "heart" is to be distinguished:
   e.g. Spruce; *Abies Smithiana.*
   (4) There is a distinct central "heart-wood":
   e.g. The Pines and the Larch.

II. Dicotyledons.

Always have true vessels (except *Drimys* and one or two rare forms), which differ considerably in size, number, and distribution. The wood is usually complex in structure, the elements (cells, fibres, tracheides, &c.), being variously disposed. Annual rings may be obvious, or indistinct, or even absent, and marked in various ways. Medullary rays always present, but differ much in number, size, &c.

A. Dicotyledons with no distinguishable annual rings; but there may be also partial zones of tissue (usually wood-parenchyma) easily distinguished as incomplete bands which

run into one another, and do not pass round the section ("false rings").

N.B.—There are no European timbers in this class; it is, on the other hand, very full of Indian and tropical timbers.

(1) Partial zones are present, running more or less concentrically as bands or incomplete rings, passing into one another here and there, and forming so-called "false rings."

(i) Medullary rays of two kinds: some very broad and easily seen without a lens, the majority fine. This may be termed the type of the Indian Oaks:

e.g. Quercus lamellosa, *Q. incana*, and some other Indian oaks.

(ii) All the medullary rays narrow and of one kind. The further subdivision of this group depends on too many characters to be enumerated in detail here, but the following important Indian timbers may be given in illustration:—

α The "false rings" of tissue are particularly distinct. This may be termed the Fig type, and its chief characteristic is unmistakable when once seen.

(i) No distinct heart-wood is formed, the timber is moderately hard and dense (weight about 40 lbs. per cubic foot), greyish.

e.g. Ficus bengalensis, *Pongamia glabra*, *Terminalia belerica*, &c.

(ii) Heart-wood dark and heavy; about 60 lbs. per cubic foot;

e.g. Prosopis spicigera.

β The false rings are obscure, and the wood particularly hard, heavy, and close-grained. This may be termed the Iron-wood type.

All have a dense red, brown, purple, or black heart (75 to 85 lbs. the cubic foot) :

e.g. Mesua ferrea, *Heritiera littoralis*, *Xylia dolabriformis*, *Hardwickia binata*, *Terminalia tomentosa*, *Dyospyros Melanoxylon*, &c. These are the chief hard woods of India.

γ The following (and others) are less easily classified, and other characters have to be used in grouping them :

e.g. Dalbergia Sissoo, *D. latifolia*, *Bassia latifolia*, *Melia indica*, *Acacia arabica*, *A. catechu*, *Lagerstroemia parviflora*, *Pterocarpus Marsupium*, &c.

(2) No such partial zones or "false rings" are evident ; the wood is practically devoid of annual rings (though microscopic examination of thin sections may show traces).

(i) Soft wood ; no heart-wood formed ; grey (Bombax type) :

e.g. Bombax malabaricum, Mango.

(ii) Heart-wood usually present, and the woods denser and less porous :

e.g. Albizzia Lebbek, *Schima Wallichii*, *Zizyphus Jujuba*, *Tamarix articulata*, *Adina cordifolia*, *Dipterocarpus tuberculatus*, &c.

B. DICOTYLEDONS in which the annual rings are always distinguishable, and usually obvious, though they may be very narrow. These rings are marked in two chief ways, and a little practice enables the student to distinguish them easily in most cases.

(*a*) The annual rings are particularly clear, because the vessels in the spring wood are either larger than

elsewhere, or they are numerous and crowded, whereas the vessels in the autumn zone are small or few and scattered.

(1) The vessels on the inner side of the spring wood in each annual ring are large and conspicuous. (Many of our European timbers come here.)

The various types are further distinguished by the characters of the medullary rays, and the mode of distribution of the vessels, &c., in the autumn zone.

(i) Some of the medullary rays are broad, and easily visible to the naked eye :

e.g. Quercus Robur, &c., the Oak type.

(ii) All the medullary rays are alike, and fine. (The further subdivision depends on the arrangement of the autumn vessels, &c.) :

e.g. the Ash, Elm, Chestnut, and the following Indian timbers :—Teak, *Cedrela Toona*, *Melia Azedarach*, *Lagerstræmia Reginæ*, &c.

(2) The vessels on the inner margin of the spring-wood are not larger than elsewhere, but they are more numerous and crowded than in the autumn wood, and hence render this zone porous in another manner.

e.g. Plum, Elder, Lilac, Buckthorn, &c., and the following Indian timbers :—*Santalum album*, *Gmelina arborea*, &c.

(*b*) The annual rings are distinct, but the line of demarcation is due to the close texture of the elements composing the autumn wood, and not to conspicuous differences in the sizes or distribution of the vessels, hence the annual zones appear to be divided by firm thin lines. (Most of our European timbers come here.) The chief types

are afforded by the following, and they are distinguished further by minor details of structure, colour, density, &c.

(i) The vessels are visible without a lens, and scattered ;
e.g. Walnut, *Shorea robusta.*

(ii) The vessels are minute, and usually numerous.
The wood (at least the heart-wood) is hard.
e.g. Beech, Birch, Box, Maple, Plane, Hornbeam, *Eugenia Jambolana*, *Chloroxylon Swietenia*, *Anogeissus latifolia*, *Schleichera trijuga*, *Ægle Marmelos*, &c.

The wood is soft.
e.g. Horsechestnut, Willow, Poplar, Alder, *Populus euphratica*, *Michelia excelsa*, *Holarrhena antidysenterica*, *Dillenia indica*, *Boswellia thurifera*, &c.

CHAPTER IV.

ON THE THEORIES ADVANCED TO EXPLAIN THE ASCENT OF WATER IN TALL TREES.

It has often been remarked that no account exists in any English work, of the recent views as to the mechanism which lifts water to the top of tall trees, or of the controversy which has been so eagerly carried on for some years on this subject, and, considering the numerous interesting observations and experiments which have been made in this connection, some general account of the matter should be of interest both to students and teachers. In view of the necessity that some botanist should undertake the task, and that it ought to be done soon because the phenomena have so many bearings upon matters now engaging the attention of biologists, I have attempted it, especially because so many side-lights

on the structure and functions of timber turn up by the way during the discussion. It is true, the subject demands the combined efforts of the physicist and the botanist for its complete treatment, but it has seemed possible to give a general account of the whole controversy, without necessarily entering into those side issues which turn upon the more purely physical and mathematical points. With respect to the importance of the subject to the physiologist there is no need to say more than that it has points of contact and suggestion with almost every department of that vast study.

In and about the year 1860, much light had been thrown on the subject of capillarity, and, for our purposes, especially by the researches of Jamin,[1] who thought he could show that the ascent of water in a tree was simply a capillary phenomenon, the vessels &c. in the stem being the capillary tubes concerned.

If a capillary glass tube is placed with one end in water, the surface of the column which rises in the tube is concave, as is well known, owing to the adhesion between the glass and the water; the concave surface may be regarded as a film, which exerts pressure on the interior of the liquid, but which pressure is smaller than it would be if the film were plane. Hence the

[1] See, for instance, Comptes Rendus, 1860, t. 1, pp. 172, 311, 383.

pressure on the column exerted by the water outside is greater than that inside, and the water rises in the tube till equilibrium is established. For tubes of the same material this capillary ascension is inversely proportional to the diameter of the tube. If we take a long capillary tube filled with alternate bubbles of air and columns of water (such a system is called a *chapelet de Jamin*) it will be found that even huge pressures at one end exhaust their effect before the other end is reached—each of the columns of water shows less and less effect. In each partial column, the anterior end becomes *more* concave, the hinder end *less* so; *i.e.* we have two unequally curved films exerting different pressures on the interior of the column in each case, the pressure of the hinder (less concave) surface being larger opposes the external pressure with considerable effect. Hence the pressure conveyed by the first bubble to those in front, is less than that exerted at the opening of the tube; the pressure of the second bubble on the third less still, and so on till the visible effect has practically disappeared before the other end of the tube is reached.

It was concluded from Jamin's researches that a water-column of any height may be held upright if in a fine tube and broken by a sufficient number of air bubbles; and if the tubes are alternately

thicker and thinner, the *chapelet de Jamin* is even more effective.

Jamin has shown, further, that porous bodies such as gypsum, absorb water with a force equal to a pressure of several atmospheres: when such bodies are saturated, they are practically impervious to air, though easily permeable by water. Hence a block of gypsum may be fixed to each end of a glass tube, the apparatus saturated with water and the tube filled, and if the lower block of gypsum is placed in wet sand and the upper exposed to the air, the evaporation at the exposed end is compensated by a flow from below.

Jamin thought this explained the ascent of water in plants, and that the lumina of the vessels, &c., corresponded to the capillaries of his system. Hofmeister on the contrary thought the experiment confirmed Meyen's view that the water passes up as imbibed water—supposing the wood-walls to correspond to the porous body. We shall see how Sachs has extended this idea; but it should be clearly apprehended that Sachs's idea of imbibition is a very different one from the old notion of its dependence on capillarity. In a capillary system there are pores, and air may be driven out: the water of imbibition is inter-molecular (or at most inter-micellar) water.

Such were some of the views which led gradually

towards the modern ideas of imbibition. Sachs in his *Experimental-Physiologie*, took both views into account, and thought that capillarity as well as imbibition came into play. In 1868 Unger[1] concluded that the water does not ascend in the lumina of the vessels, &c., but that it passes up as water of imbibition in the substance of the cell-walls; and Sachs, in the fourth edition of his *Lehrbuch*, definitely threw over the capillary theory, and assumed that the water moves either entirely as water of imbibition *in* the substance of the walls, or (as Quincke had suggested) as a thin film of water *on* the inside of these walls.

Meanwhile observers had begun ranging themselves more or less into two groups as it were. Boehm[2] in 1864 suggested that the elasticity of the epidermal cell-walls would come into play, and affect the pressures on and in the air-bubbles in the cavities of the elements: and Theod. Hartig[3] had insisted upon the alternate expansions and contractions of these air-bubbles as important factors in causing water to move from cell to cell.

From other points of view Von Höhnel showed[4]

[1] *Sitzungsber. d. Akad. d. Wissensch. zu Wien*, lvii. abth. i. 1868.

[2] *Sitzungsber. d. kaiserl. Akad. der Wiss. zu Wien*, b. 50 i. (1864).

[3] *Bot. Zeitg.*, 1861, p. 18.

[4] *Jahrb. für Wiss. Bot.*, 1879, b. 12, p. 77.

in 1879 that if a transpiring branch is cut under water, the air presses the water with considerable rapidity into the vessels.

So much by way of introduction. I now propose to start with the position of affairs in 1882, the year in which Sachs's *Vorlesungen über Pflanzen-physiologie* first appeared.

At this time it was allowed by all that the water which ascends the stem of the tree passes from the roots to the leaves in the wood—that it is absorbed by the root-hairs, traverses the roots to the stem, and passes up the wood to the leaves, whence it passes off by transpiration. It was also agreed that the main flow takes place in the "sap-wood" (alburnum), because the simple experiment of "ringing" the stem proved that with most trees the flow is seriously diminished, or stopped, if the outer wood is removed as well as the cortex, whereas no harm ensues if the alburnum is left intact: moreover, observations on hollow trees showed that the inner parts of the timber are not necessary to the ascent of the water.

Further points of agreement were found in the knowledge of the structure of wood—the annual rings, medullary rays, the differences between duramen and alburnum, the properties of the cambium, &c. It was also known that while the secondary wood of

Conifers has no vessels, but consists almost entirely of tracheides with bordered pits, the vast majority of Dicotyledons and Monocotyledons always have vessels in addition to other elements—tracheides, libriform fibres, and wood-parenchyma. The proportions of the latter vary, and one or more kinds may be absent.

Less unanimity appeared as to the properties and functions of the elements of the wood, and in fact the whole controversy at one time turned upon this question. It had been discovered that, broadly speaking, the vessels contained less water and more air in the summer than in the winter, and that even in the tracheides there was usually if not always some air. Whether the vessels and tracheides were ever entirely devoid of either air or water was a disputed point. Much discussion was also still abroad as to the ultimate structure of the cell-walls of the elements, but it was common knowledge that, whereas the wood-parenchyma usually still retains its cellulose walls, protoplasmic contents, starch, &c. (and the same with the cells of the medullary rays), the walls of the vessels, tracheides and fibres are lignified more or less completely, and soon lose their living contents.

Since most of the other points of importance to the controversy were either disputed or imperfectly

understood, I shall defer them till such time as they crop up naturally in the argument.

As to the explanation of the ascent of the water from the soil to the leaves, two conflicting hypotheses were in the field—neglecting older views, which either simply shelved the question by speaking of a process of suction or diffusion, or tried to explain the phenomenon as due to root-pressure, or capillarity, or to the molecular movements in a thin film of water overspreading the inner surface of the elements.[1] The two prominent hypotheses were (1) Sachs's view that the water travels as water of imbibition in the molecular interstices of the lignified walls of the vessels and tracheides, and (2) the view, at the time most strenuously advocated by Boehm, that the water ascends in the cavities of the tracheides and vessels.

We will consider Sachs's hypothesis first.[2] Taking his stand on the facts already conceded, Sachs points out that we have to explain a movement by which a particle of water must travel at a rate of from fifty to two hundred centimetres per hour in the wood, and by which the leaves are supplied so copiously, that

[1] For a summary and criticism of older views see Sachs's *Text-Book*, second English edition.

[2] See his *Lectures on the Physiology of Plants*, English edition, p. 225.

they transpire in one season quantities amounting to many times the volume of the whole plant.

Taking the wood of Conifers as being the simplest and most thoroughly studied, and choosing that of the yew because it is devoid of resin-canals, he points out that the tracheides are closed cavities—the membranes of the bordered pits forming a complete septum—and hence a piece of yew wood may be employed to filter off fine particles. There being no capillary tubes here, we cannot entertain the idea of a capillary ascent: moreover, even in Dicotyledons, the sectional areas of the lumina of the vessels are too large to admit of an ascent by capillarity beyond a few yards at most.

But now comes a weighty argument. At the time when transpiration is most active in the summer, and therefore when most water is passing through the wood, the cavities of the tracheides and vessels are not full of water, but contain very little, and the vessels may even (so Sachs asserts) be empty: hence the wood floats on water, which it would not do unless considerable air-cavities existed. The presence of the air can also be proved by warming the wood, and the phenomenon of "water-logging" depends on the gradual filling of the cavities by water, which soaks in and displaces the air.

Hence, at the time when most water is ascending through the wood, the cavities of the elements contain much air (and no doubt vapour). The determination of the specific gravity, shows that the *substance* of the wood cell-walls is heavier than water in the ratio of 1·56 to 1 ; and of course it was easy to determine how much water a given piece of wood contained, and it was found by this method also that the water could not have been held in the walls: it also showed that some of the water was in the cavities.

Sachs then, by the ingenious method of finding how much water is absorbed when a piece of dry wood is suspended in vapour, determined that the elements imbibe by means of their lignified cell-walls, to the extent of half the volume of the latter.

Based on a long series of such investigations,[1] Sachs finally came to the conclusion that the lignified walls of the wood-elements have certain remarkable molecular properties : that they absorb relatively but little water, *but that this water is wonderfully mobile.* On this assumption he gave to the world his daring hypothesis, which is that the water in the molecular interstices of the walls of the tracheides, vessels, &c. moves upwards to compensate that lost by transpira-

[1] See Sachs's *Über die Porosität des Holzes*, Würzburg Arbeiten, ii. 1879.

tion, because the slightest displacement is sufficient to disturb the equilibrium of the whole continuous column of water.

Of course the great advantage claimed for the hypothesis was that it did away with the difficulty presented by the height of tall trees. Sachs supposes the molecules of water to be as it were dissolved in the substance of the cell-walls, held by molecular forces in the same way that a particle of salt is commonly supposed to be suspended between molecules of water in a solution ; and just as any particle of salt in the ocean, for instance, is free to move in any direction—to and fro, or up and down—and quite independently of gravitation, so he thought his molecules of water could be regarded as infinitely mobile between the particles of the cell-wall. It matters not whether we regard the cell-wall as composed of *micellæ*, or aggregate molecules, or other structural units, in this connection, as the hypothesis simply turns on the freedom of movement in spaces beyond the ken of rough physics.

When we come to experiments offered in support of this hypothesis, the weak points come out somewhat vividly.

If the stem of a hop, flax, &c., be sharply bent on itself, the cavities of the vessels, &c. are of course com-

pressed : Sachs assumed that they were closed entirely, and that the fact that the leaves above still transpired proved the truth of his assumption—the water moves in the substance of the cell-walls, because there is here no other passage open to it. If a branch is cut and allowed to dry, the power of conducting water is lost—a dry stick placed in water may become gradually saturated, but it has lost the power of *conducting* the water. Sachs explained this as due to some molecular change in the substance of the cell-walls. To the same cause he attributes the gradual loss of conductivity noticed when the cut end of a fresh branch is immersed for some time in water. Those familiar with the literature will have noticed that Sachs did not regard several facts then known, and bearing more than indirectly on his hypothesis.

For instance, if a shoot is cut and placed with the cut end in water in one leg of a U tube, and allowed to droop, it is often possible to restore the turgid condition of the upper tissues, by forcing water in under the pressure of mercury poured into the other leg of the U tube.

Again, at the time when transpiration is most active in the summer, it was found by Von Höhnel that if a shoot is bent gently down, and cut through under water, or a coloured solution, or even mercury, the

liquid rushes up into the vessels under a pressure which must be regarded as considerable: this is due to the fact that the air in the tracheides, vessels, &c., is rarefied, and the pressure just referred to is the difference between that of the contained air and that of the external atmosphere. Of course Sachs viewed all such cases as only going to show that when the leaves are taking water rapidly from the cell-walls, the latter supply themselves from whatever surplus water may exist in the cavities, and, since air cannot pass through the wet membranes or only to a very slight extent, the contained air-bubbles expanded, and so on. Sachs attributes to these air-bubbles, however, some influence in drawing water into the cavities.[1]

An old experiment of Theod. Hartig's should be mentioned here. If a piece of the stem of a Conifer, a yard or more long and with the ends cut clean across, is held vertically, and one drop of water is placed on the upper section, a similar drop appears at the lower end in a few seconds, enlarging in proportion as the upper one sinks into the wood: this is regarded by Sachs as a proof generally of the easy permeability of wood. I shall have occasion to refer to this experiment of Theod. Hartig's several times in the course of the discussion, as some important matters turn on its

[1] *Vorlesungen über Pflanzen-physiologie*, p. 322 (Eng. Ed. p. 269).

explanation. I now pass to the *résumé* of the alternative hypothesis, that the water ascends in the cavities of the tracheides, vessels, &c., and not in the substance of the cell-walls.

In 1881, Boehm published a paper on the subject,[1] which, whatever its shortcomings from the physicist's point of view, must be quoted in order to show the direction of thought on the side of those who could not accept Sachs's assumptions.

Boehm pointed out that the existence of the "negative pressure" in transpiring plants puts osmosis out of court as a cause for the ascent of the water in the wood: he also agrees with those who reject all capillary hypotheses. He then advances the following criticisms; (1) the wood contains more water than can be contained in the walls; (2) if cylinders of wood are cut so that their long axes are parallel to a radius of the stem, or to a tangent of the same, then the easy pressure of water in the direction of their longitudinal axes (which is known to occur in cylinders with their long axes co-incident with the axis of the stem) is no longer possible. In other words, it takes a much greater pressure to drive water across the stem, either tangentially or radially, than it does to drive

[1] *De la Cause du movement de l'eau*, &c. (Ann. des Sc. Nat. vi. ser. t. xii., 1881.)

it in the direction of the long axes of the elements. (3) Cuttings of willows &c., will, when transpiring, exert a pull (so to speak) on mercury, to such an extent as to raise a column sixty mm. in height. (4) Fairly thick longitudinal sections of fresh branches can be so arranged under the microscope as to show that air-bubbles, under feeble pressure, exist in the vessels and tracheides. Placed in water, the bubbles contract—*i.e.* water is forced through the damp walls, which are impervious to air. It may be mentioned, by the way, that a rough illustration of the imperviousness of a wet membrane to air is to be seen in any wash-tub, where the imprisoned air drives up the wet linen into rounded hummocks as the laundress pushes various parts deeper into the water. (5) Boehm rightly lays stress on the importance of Von Höhnel's discovery[1] that the pressure in the vessels in summer may be so low, that it does not exceed ten cm. of mercury. (6) He then points out the bearing of his previous papers on the whole subject (of which the present is practically a summary), and his own numerous observations,[2] and among others notes the following.

[1] Haberlandt's *Wiss. prakt. Unters auf den Geb. d. pflanzenbaues*, t. xi., 1877.

[2] Of course it is impossible to quote here all that bears on this question, but the chief of these papers are in *Landw. Versuchs. Stat.*

Theodore Hartig's experiment with the piece of stick shows (Boehm thought) that the drop of water causes a long column to move: if, however, the vessels or tracheides are first injected with mercury, it requires great pressure to cause movement of the column, and the experiment fails. Finally, Boehm denies that the vessels or tracheides are ever totally devoid of liquid water; even when the transpiration is most active there is always some water as well as air present.

Boehm then puts forward his own hypothesis to explain the water current in tall trees. The cells of the transpiring surfaces (such as the leaf epidermis) have elastic walls, and when they lose water by evaporation, the pressure of the atmosphere tends to drive these walls inwards, whereas their elasticity tends to make them resume their previous shape and positions. Hence an aspirator action is exerted on the cells below, the elastic walls acting like valves. Water is taken from the cells below, and this reduces the pressure on the imprisoned air-bubbles: this being so, the air-bubbles in the cavities still lower in the plant are under slightly greater pressure than those in the cells just considered, and they will expand

1877, t. xx. pp. 357–389; *Jahrb. für Wiss Bot.*, 1877, p. 120; *Ann. d. Sc. Nat.*, 1878; *Warum steigt der Saft in den Bäumen?* Wien, 1878; *Bot. Zeit.*, 1879, p. 225.

and drive water up. In this way a suction-pump-action was supposed to be transmitted from above downwards, from leaves to roots, and here the necessary water passes in from the soil, under atmospheric pressure.

Boehm points out that in any vessel there is a series of air-bubbles at more or less regular distances, and separated by capillary columns of water. In fact the vessel constitutes a veritable *chapelet de Jamin*, where the surface actions are so powerful that even enormous pressures will not move the column as a whole, though there is no difficulty in supposing parts of the capillary columns of water to pass through the permeable cell-walls if the neighbouring air-bubbles undergo alterations of pressure.

A point on which Boehm laid some stress, by the way, is the blocking up of the passages by means of *tyloses*, ingrowths of surrounding parenchyma-cells which push through the bordered pits of the vessels, and fill their cavities with a spurious tissue. It is (says Boehm) these tyloses which render the heart-wood impervious or nearly so, and it is they also which gradually block up the vessels of cut branches.

A few words as to Boehm's views regarding the origin of the air-bubbles and their reduced pressure. The air enters in solution at the root-hairs, at the

pressure of one atmosphere. The aspirator-action of the cells in the leaves reduces the pressure, and the bubbles separate and experience relatively enormous friction. Morever, the oxygen of the air will be absorbed by the cells, and an equal volume of carbon-dioxide will be returned: this is soluble in the water, and is carried in solution to the transpiring surfaces. Hence is seen a further cause for the reduction of pressure in the bubbles, and an important aid in the sucking action: the bubbles at length consist entirely or almost entirely of nitrogen under a pressure of considerably less than an atmosphere.

It will be seen that the fatal defect in Boehm's hypothesis is the assumption that water can be raised to such enormous heights, as it must be in tall trees, simply by differences of atmospheric pressure, when we know that the pressure of one atmosphere is balanced by a column of water a little over thirty feet in height. However, as the faults in the above views will come out best in the controversy which follows, I will not dwell further upon the matter here.

The next important contribution to the subject, in order of publication, was a paper by Fr. Elfving[1] which appeared in 1882.

Elfving classifies the adherents of the two hypo-

[1] *Über die Wasserleitung im Holz*, Bot. Zeit. 1882, October.

theses as follows. Unger, Pfeffer and Sachs may be regarded as the exponents of the imbibition theory; while Hartig, Naegeli and Schwendener, and Boehm are the chief adherents to the view that the water ascends in the cavities or lumina of the vessels and tracheides—the only general point of agreement between the botanists last mentioned, however, being that the lumina constitute the route of the water, for they differ greatly in details.

Elfving set himself the task of subjecting the two rival hypotheses to experimental tests. He employed the wood of the yew, unless otherwise specified. Having verified Th. Hartig's experiment, he attached a piece of yew branch, a few centimeters long and about one centimeter thick, to the end of a piece of caoutchouc-tubing, and showed that very gentle blowing and sucking through the tube caused the alternate expulsion and withdrawal of water, at the cut face of the alburnum.

He then showed that the yew-wood is readily permeable to all kinds of fluids, very little pressure being needed to drive the following in succession through the same piece, and in the order given—viz. water, alcohol, benzol, alcohol, water, dilute ammonia, water, dilute acetic acid, water, alcohol, &c. Under *great* pressure he could even drive a solution

of gum through. He points out that this easy permeability is not suggestive of imbibition.

If a piece of the yew branch is taken fresh, fastened to a tube, and the wood of the alburnum exposed by removing a clean longitudinal slice, then it is possible to see the air-bubbles in the tracheides expand and contract under the microscope, if the observer alternately sucks and blows through the tube. Similarly, by merely blowing down one leg of a U tube containing eosin solution, the dye can be forced through a piece of yew-branch fastened to the other leg; on afterwards splitting the wood, the alburnum alone is dyed, and the dye is *in the cavities of the tracheides*, between the air-bubbles, the substance of the lignified walls not being stained except at the cut ends. This and similar experiments proved that the eosin solution did not traverse the lignified parts at all —it filtered from tracheide to tracheide through the unlignified membranes of the bordered pits, the only part stained.

As is now well known, these bordered pits of the Conifers occur almost exclusively on the radial walls of the tracheides, a very few being formed on the outer tangential wall of the last rows of tracheides formed in autumn. Elfving argued that if the fluid travels *viâ* the bordered pits, then it ought to be possible

to make it traverse the wood tangentially, but not radially.

He therefore had cylinders of sap-wood turned, in such a way that the long axis was (1) parallel to a radius of the stem, (2) parallel to a tangent, *i.e.* in a plane at right angles to No. 1, and compared their behaviour with (3) cylinders whose axis was parallel to the axis of the stem. The cylinders were all the same size, turned fresh, and kept moist: they were placed on one end of a U tube, and a solution of eosin driven through by the pressure of mercury in the other leg of the tube. The longitudinal cylinders (3) allowed the eosin to pass with the slightest pressure so long as they were cut *from the alburnum* —the same cylinders cut out of the *duramen* were almost impervious.

The tangential cylinders (2) allowed the eosin to filter through *slowly*, under a pressure of seventeen cm. of mercury. But not a drop could be forced through the radial cylinders (1) under the same pressure. Even forty cm. of mercury failed to force water through these cylinders.

This proved that the alburnum transmits water in the tangential direction, but not in the radial direction. Even in the tangential direction, however, the water filters through much more slowly, because, the

tracheides being about two mm. long, and only, say, $\frac{1}{50}$ mm. in diameter, the fluid in the longitudinal cylinder (3) has only five barriers interposed for each centimeter of length, whereas the tangential cylinder (2) offers five hundred barriers for each centimeter of length.

Elfving then showed that if one uses thin plates (one to two mm. thick) of the wood, the water passes through as easily in the tangential direction as in the longitudinal: whereas plates equally thin, but cut in the plane of a tangent to the stem, will not allow water to pass even under considerable pressures. There is no mistaking the significance of the coincidence that the water will pass so long as it meets bordered pits, but will not pass in directions where it meets none.

Elfving recognised, however, that the partisans of the imbibition theory might reply that these experiments only demonstrated that the cell-walls transmit differently in different directions, and that it was necessary to test the alleged conductivity of the cell-walls directly.

He did this by the ingenious method of forcing cacao-butter—which melts at 30° C., and does not injure the walls—into the cut end of a piece of wood. By colouring the cacao-butter with eosin, it was easy

to see that a slight pressure forced it into all the cavities of the alburnum exposed by the section, and even through the bordered pits, to a height of ten mm. In this way he *blocked up the lumina of the tracheides*, and allowed the cacao-butter to congeal; he then cut a clean surface exposing the clean-cut walls of the tracheides. A pressure of *sixty cm. of mercury* failed to force water through, whence Elfving concluded that apart from any possible molecular movements of water imbibed in the cell-walls) the rapid currents of water in the wood take place through the cavities and not in the substance of the cell-walls.

Elfving then goes on to discuss some other phenomena, showing that water is held in the vessel of *Aristolochia*, for instance, by exactly the same force as it is held in a capillary tube of like calibre, and that the tracheides and bordered pits are very impervious to air.

A piece of wood 3 cm. long allowed water to pass easily under a pressure of 1 cm. of *water*, whereas the pressure of a column of *mercury twenty cm.* high failed to drive air through. Now since one cm. of water exerts a pressure roughly equal to $\frac{1}{1000}$ atmosphere, we have to conclude that the slightest rise of pressure due to the expanding of an air bubble in a tracheide, will drive water through.

Elfving's confirmation of the negative pressure of the air in wood is interesting. Among other experiments was the following: A transpiring branch was cut under water, and as rapidly as possible transferred to eosin, and a fresh cut made under the surface of the dye: that a strong "suction" still existed was proved by the taking up of the dye to a height of $2\frac{1}{2}$ cm. in the alburnum. He then shows that cut branches, transpiring freely, take up eosin, and that on examining with the microscope, all the evidence (as before) goes to show that the liquid ascends through the cavities. It is interesting to note that in these experiments the medullary rays, the cells of which communicate with the tracheides by means of bordered pits, were coloured deep red by the eosin; indeed in the upper part the rays had taken all the colouring matter.

As drying proceeded, the wood lost its conductibility, but to the last Elfving found the coloured fluid held in the borders of the pits, whence he concluded that one function of the ring-like border is to retain a capillary drop, so that however threatening the drought may be, the pit membrane retains its moist condition to the last.

The cacao-butter experiments were then applied to the sclerenchyma strands of the Monocotyledons, which

Sachs and others assumed to be the conducting agents here—the result was as before, and I may pass over the details. The same with Dicotyledons, and here again it is interesting to note that the injected cacao-butter penetrated through the vessels, not only into surrounding elements, but into the starch cells of the medullary rays. Mere sucking brought the fat up the vessels and *into the tracheides, &c. surrounding them.*

Elfving expressly points out that this remarkable injection of the xylem-parenchyma and medullary rays always occurred by merely *sucking* with the mouth, though afterwards a *pressure* of 25 cm. of mercury failed to drive water through. Elfving's conclusions are that wood loses its "conductibility" as soon as the lumina are blocked, and that the rapid ascent of water under consideration does not take place in the walls of the elements. Since tracheæ in the widest sense (*i.e.* vessels and tracheides) are the only elements which never fail, and are sometimes the only elements present in the wood, and since they always contain some water, and are provided with the easily permeable pits, he concludes that they are the conducting elements. The bordered pits are filters, the ring being a support: the same is true for the rings of the spiral, the thin parts acting as pit-membranes.

The solid thick parts are necessary to prevent crushing, and the thin places are always easily permeable to water but not to air. As regards the parenchyma cells of the wood, their protoplasmic contents point to their having some other duty to perform, but they may also be employed : so also with the medullary rays.

On the whole Boehm's idea seems to be most in accord with the facts so far, the easy permeability for water and the resistance to the passage of air being the chief factors. Nevertheless, one seems to see that Elfving was too wide awake to the obvious physical defects of Boehm's theory to give it his support further than the foregoing implies. Here, again, however, I leave further remarks and criticisms to develop naturally in the course of the controversy.

I may now take together two papers by Robert Hartig[1] which appeared in 1882 and 1883 respectively. The conflicting views then abroad led him to examine the question of the distribution of air and water in wood, and some interesting discoveries were made by the way. In the first place he found that the duramen always contains water, though it is incap-

[1] "Ueber die Vertheilung der organischen Substanz, des Wassers und Luftraumes in den Bäumen, und über die Ursache der Wasserbewegung in transpirirenden Pflanzen." *Unters. aus d. Forst. Bot. Inst. zu Munchen* ii. and iii.

able of transmitting it up the stem ; but he also found that some trees—the birch for instance—never form any true "heart-wood" (duramen) at all, but consist throughout of "sap-wood" (alburnum), the inner layers of which only differ from the outer in being somewhat less permeable to water.

Hartig also convinced himself that it is the elements with bordered pits, and especially the tracheides, which conduct the water.

The absorption of the water at the roots has no direct relation to the ascent of water in the stem, being due entirely to the osmotic action of living cells —especially the root-hairs. Only in cases where the imprisoned air expands and exerts pressure, or contracts and facilitates the flow of water into a vessel, &c. need we take any account of the root action. But this root-action, which is especially favoured by a rise of temperature in the soil, helps to explain a phenomenon which has been overlooked, viz. that in the summer, in spite of the fact that transpiration is then most active, most of the trees (beech, oak, larch, Scotch pine and spruce) examined, contained their maximum of total water : the birch alone was an exception, because its period of vegetative activity is earlier.

If the tree contains so much water that the air in the cavities of its tracheides, &c. is at a pressure equal

to that of one atmosphere and if the roots still continue to absorb water in greater quantities than the leaves transpire it (as may actually occur), we have the phenomenon of "weeping" or "bleeding": similar effects are produced when the sun's rays directly raise the temperature of thin twigs—the expanding air-bubbles drive water before them, as had already been shown by Sachs and others. Hartig concludes that the cause of the ascent of the water in a tree is to be found in the differences of pressure (density) of the air-bubbles imprisoned in the tracheides, &c.: the water is driven from lumen to lumen in the direction of least pressure.

Taking the simple tracheide system of Conifers, the elements are in contact on the one hand with the mesophyll of the leaves, in the venation, and on the other hand with the parenchyma of the roots; the walls in contact are the thinnest of all, and water easily filters through them, but they need strengthening lattice work—the *raison d'être* for rings, spirals, &c., and it is interesting to note that this kind of support only occurs in the proto-xylem, the part which alone comes into direct contact with the above-named cells. The trunks of trees, &c., would be impossible, however, if the secondary wood were not provided with more support; hence we find firm, thick-walled organs in it,

the walls of which are almost impermeable to water. Elfving's experiments prove that no such easy mobility of the imbibed water, as Sachs assumes, exists; and Hartig confirms the view that the water only moves through the membranes of the bordered pits.

These delicate closing membranes are very elastic, and when extended by pressure are particularly thin and permeable; the solid ring-border is a support so arranged that when the delicate membrane is driven too far it rests on the inner surface of the ring, and the torus blocks up the pore, the apparatus thus acting as a safety-valve to prevent undue tension or rupture of the filter-membrane.

In Dicotyledons water can be more easily forced in a radial direction than in Conifers, because the bordered pits are not confined to the radial walls; but even in Conifers the last-formed tracheides of each annual ring have numerous very small bordered pits on their tangential walls, no doubt to serve as water-doors to supply the cambium in the spring, as otherwise it must suffer. Finally, it should be noted that in the Conifer the long, prismatic tracheides are arranged in the annual ring in radial rows, those in each radial row being equal in height: tangentially, however, the rows stand at unequal heights, so that anything passing through the bordered pits (on the

radial walls) from tracheide to tracheide, would go by steps spirally round the stem as up a spiral stair-case. It is this last-mentioned position which renders possible an ascent of the water from lumen to lumen of the tracheides.

Now, as a mere matter of observation, determined by finding the quantity of water, &c. in all parts of the wood at regular heights in the tree, the tracheides always contain some water and some air, but the quantities of each differ considerably both according to the part of the tree and according to the season. In all cases the walls must be saturated with imbibed water. In the Dicotyledons, &c. the liquid water in the lumina of the vessels and tracheides occupies at least one-third and often two-thirds of the volume of the lumina: in the Conifers, the tracheides may have only two-thirds of the lumina occupied by water, but as much as nine-tenths may occur. The remaining portions of lumen are filled with air, and perhaps the most valuable of Hartig's contributions to the question was his patient and ingenious determination of the fact that the actual air-contents of the tracheides, &c., *decreases from below upwards:* that is to say, if we suppose the air to be at the same pressure throughout, the amount of water in the lumina of the tracheides, &c. increases as we ascend the tree.

No less important was the discovery that the air is *not* at equal pressure throughout, but that it is *less dense in the upper parts* of the tree than in the lower.

Hartig's views, as then expressed, were as follows: The water, enclosed together with air in a tracheide, &c., is supported in the tubular cavity by capillarity, so that its weight cannot make itself felt downwards through the closing membranes of the bordered pits; in true vessels the individual water-columns are suspended, separated by air-bubbles. When transpiration is active, and the amount of water in the tree tends to diminish, the air in the upper parts becomes much more rarefied than that in the lower: for instance, in the wood of the branches of the crown, the air may be expanded to five times its original volume, while that in the lower parts of the stem expands simultaneously to only twice its volume.

This diminution of pressure as we ascend must exert a relatively powerful lifting force from tracheide to tracheide, the greater pressure of the air below driving the water through the membranes of the bordered-pits.

If the supply of water from below is arrested (as was done in an old spruce by sawing to the depth of the non-conducting inner wood) the density of the air slowly becomes equalized throughout the whole

system, and all movement of the water ceases—the leaves and cortex in the upper parts of the tree dry up and death may ensue. In the case of the spruce mentioned this occurred *when the lumina of the tracheides contained liquid water to the extent of* 75% *of the whole volume.*

The more slowly water is being absorbed by the roots below, as compared with energetic transpiration, the more the air becomes rarefied, even in the lower parts of the tree; and the difference of pressure between the air above and that below may become so small that the water ascends only very slowly. On the other hand, the more energetic the root-action, the denser the air in the lower tracheides becomes, being pressed by the water behind. When active transpiration follows upon this state of affairs (as in the early summer) we have the greatest difference in the pressures set up—transpiration rarefies the air-bubbles above, and root-pressure compresses them below—whence the water ascends rapidly. Moreover this conduces to a continuance of rapid transpiration, for leaves transpire more freely when turgid.

On the other hand, the ascent and transpiration of water act in no appreciable way on the process of absorption: the osmotic activities at work are practically independent of such pressures and strains

as have been considered. And again, the atmospheric pressure outside the plant has no appreciable effect on the process; it is controlled and regulated by alterations in the density of the imprisoned air.

Hartig's methods of observation are worth a short description here, because they give not only insight into several peculiarities of wood, but also an idea of the very different points of view involved.

In the forest, on the spot where the trees were felled, the pieces of wood to be examined were chosen and at once weighed, because they rapidly lose weight after exposure to air. In choosing them, the usual plan was to cut up the trunk into blocks, and to select blocks from the various heights, about 2—3 meters apart, splitting them up as follows: two opposite wedge-shaped segments were cut out of the circular block, and each separated into three parts —the inner part comprising the heart-wood, the outer part sap-wood, and the middle one both sap-wood and heart-wood. The pieces thus obtained weighed from 300 to 700 grams each, and after weighing were packed and despatched to the laboratory.

Here, the first thing to do was to determine the volume in the fresh state,[1] which was done by reading

[1] Since the wood does not shrink sensibly until it has lost much water, it was not necessary to do this in the forest, but it was done next day.

the amount of water they displaced. A discussion as to the sources of error leads to the conclusion that they do not amount to more than about 0·5 per cent. on the average. The pieces of wood were then dried for some weeks. Some interesting observations were made, confirming the conclusion that so-called air-dry wood gives various weights according to the condition of the atmosphere, and therefore of little or no scientific value.

The drying was then completed in a hot-chamber at 105—110° C, and the dry weight registered: the loss in weight of course registered the amount of water contained in the wood.

The next thing was to obtain the volume in the dry state, in order to estimate the shrinkage; this was done, as before, by displacement, several careful precautions having to be taken.

So far, the following data were to hand:

1. The specific weight (fresh)
$$= \frac{\text{Absolute weight (fresh)}}{\text{Volume (fresh)}}.$$

2. The specific weight (dry)
$$= \frac{\text{Absolute weight (dry)}}{\text{Volume (dry)}}.$$

3. The shrinkage
$$= \frac{\text{Volume (fresh)} - \text{volume (dry)}}{\text{Volume (fresh)}}.$$

4. The weight of the organic wood-substance (+ traces of ash) per volume (fresh)

$$= \frac{\text{Dry weight}}{\text{Volume (fresh)}}.$$

5. The amount of water in the volume (fresh)

$$= \frac{\text{Weight (fresh)} - \text{dry weight}}{\text{Volume (fresh)}}.$$

6. The amount of water in 100 units of the fresh weight

$$= \frac{\text{Weight (fresh)} - \text{weight (dry)}}{\text{Weight (fresh)}}.$$

Sachs had already shown in his paper on the *Porosity of Wood*, that the specific gravity of the solid wood-substance is 1·56, a number that was obtained by heating small pieces of wood in solutions of neutral salts to drive out the air, and then finding the specific gravity of the solution in which the wood *just* begins to sink. Hartig repeated these experiments with birch, beech, oak and pine, both heart-wood and sapwood, and found that they all remained for days floating quietly at any level in a solution of calcium nitrate of specific gravity 1·555, whence we may regard Sachs' number as confirmed. With this further datum, we get

7. The percentage volume occupied by the dry wood-wall per volume (fresh)

$$= \frac{\text{Weight of organic substance per 100 volumes (fresh)}}{\text{Sp. gr. of wood substance (\textit{i.e.} 1·56)}}$$

Then, subtracting the dry volume and the water from the fresh volume, we get

8. The volume occupied by the air-spaces in the wood.

But we have still to determine how much of the total water is imbibed in the cell-walls, and how much exists in the liquid state in the cavities of the tracheides, &c. It may be safely assumed that as long as any liquid water exists in the lumina, the walls will be saturated. Sachs' method of hanging a piece of wood, dried at 105° C. in an atmosphere saturated with moisture, was employed. The temperature was kept constant, and it was found that in two days the wood had absorbed water to the extent of half the quantity it was capable of absorbing, and it then went on absorbing it more and more slowly, until it took no more.

Hartig concluded that the capacity for imbibing stands in intimate relation to the presence or absence of cells containing substances which swell in water.

For instance, the inner wood ("heart-wood") of beech continued to imbibe for forty-seven days, and then had taken up 57 per cent. of its substance-volume; while the alburnum of beech, which contains much starch, continued to imbibe for fifty-seven days,

and had then taken up water to the extent of 72 per cent.

Heart of oak took up 75 per cent., oak alburnum 92 per cent. of water. Birch took 66 per cent. Pine from 45 per cent. to 57 per cent. according to the quantity of resin, and so on.

It will be remembered that Sachs hung a dried, and therefore cracked, disc of wood in a damp atmosphere, and regarded the experiment as concluded when the crack closed: Hartig points out that the wood goes on imbibing water long after the crack closes, to make good the shrinkage, hence his higher numbers.

The next datum is

9. The volume occupied by the saturated woody-walls (+ saturated contents) = dry volume + (dry volume × water capacity).

And, again,

10. The quantity of liquid water in the lumina of the tracheides, &c. = total water − (dry volume × water capacity).

By employing these factors and methods, Hartig obtained a huge series of numbers for each tree, tabulating the part of the tree used, the amount of organic substance, of water and of air, &c. at various

times of the year, which gave him the data for the generalisation as to the distribution and condition of the air as we ascend the tree; from the tables he constructed curve-diagrams, finally evolving his hypothesis as sketched above.

The next paper of importance is one by Dufour,[1] and consists in a deliberate attempt to vindicate Sachs' imbibition theory against the criticisms to which it had been subjected.

The author maintains that although various movements of water occur from lumen to lumen of the elements of the wood, and by filtration through the pits, these have nothing to do with the transpiration current: it is as water of imbibition in the walls that the rapid flow concerned in transpiration occurs. He considers that Elfving's experiments in no way overthrow the theory, because they only prove filtration under pressure, which is not denied: pressures of this kind, however, cannot affect the equable distribution of imbibed molecules in the cell-walls. Sachs had already insisted that the water is in a peculiar condition—infinitely mobile, but removed from the influence of gravitation or of ordinary pressures.

In regard to R. Hartig's criticisms, (1) that the

[1] "Ueber den Transpirationstrom in Holzpflanzen." *Art. des bot. Inst. in Würzburg*, 1883.

elements have always some water in their cavities, and (2) the water contained in the tracheides, &c., of the splint increases as we ascend the tree, Dufour simply seeks to show that this does not matter: it is not urged that the membranes should be in contact with much or little water, and in fact complete saturation brings about the maximum mobility of the imbibed water molecules. The water in the cavities must be looked upon as so much reserve-water, upon which the membranes can draw: how it comes there is not explained, but it has nothing to do with the imbibition-theory.

As a demonstration of the accuracy of Sachs' views, Dufour again brings forward experiments with sharply bent shoots, showing that in the majority of cases the bending of the vascular bundles on themselves closes the cavities, and water can no longer be forced through by such pressures as Elfving and others used: nevertheless, the plants did not cease to transpire and conduct water.

Dufour also employed the following method: Branches were sawn into in such a way that at two places on opposite sides of the stem, one being a little higher than the other, the whole of the tissues were severed as far as the pith: the argument was that the continuity of all the vessels, tracheides, &c.

was thus completely severed, although (the two cuts being at different levels) the continuity of the woody substance of the cell-walls and their imbibed water was not broken. In many of the cases Dufour found he could not drive water through such cut branches, and yet transpiration was not prevented and water passed the wounds.

Dufour rejects the view that this could occur by means of the tracheides, although he is not prepared to decide how far concurrent movements in the lumina may affect the matter.

Dufour points out that the "air-pressure theory" (then being eagerly discussed on all sides) presents the one insuperable obstacle that it will not account for the ascent of the water to a greater height than about 10 meters; and that it is of no use to invoke the aid of capillarity, as supporting the columns of water, for in just so far as it supports them it prevents their being driven upwards, or moved at all.

In a short paper published in Berlin in 1883,[1] R. Hartig offers his hypothesis in an amended form. In answer to Dufour, Hartig insists that the movement is usually and in the main from lumen to lumen, but admits the possibility that when transpiration is

[1] *Die Gasdrucktheorie und die Sachs'sche Imbibitionstheorie.* Berlin, 1883.

so vigorous as to drain all the liquid water from the cavities, the current may possibly pass as imbibed water. In those cases where Dufour could not press water through his sharply bent shoots, the lumina of the vessels were not quite closed, however nearly they might have been ; all that occurred was a curtailing of the supply of water for the time being, whence continued transpiration rarefied the air above the bend to such an extent that enough water was squeezed through to keep the shoot from drooping. In those cases where Dufour could only drive very little water beyond the sharp bend, it was because the cells, with their rarefied air bubbles, retained most of the water —absorbed it and held it fast.

As to Dufour's criticism that the sum of the air-pressures in the tree must be less than an atmosphere, and therefore cannot lift water more than 10 meters high, that must be conceded ; but the pressure of the air-bubbles does not perform the lifting of the columns, its work is rather to distend the elastic closing membranes of the bordered pits, so as to enable water to filter through them. The lifting is performed chiefly by capillarity, which raises the column of water particles in each tracheide.

One difficulty avowedly arises (but the imbibition theory does not explain it)—that is, why is it, when

the pressure is equal in two tracheides, that the water does not pass back, through the interstices of the cell-walls, from the higher to the lower one? Hartig assumes that the closing membranes of the bordered pits only allow water to filter thus easily when they are distended, by the pressure of the gas-bubbles. He thus proposes to reject the "air-pressure theory" altogether, and to substitute for it his "gas-pressure theory."

Vesque, in 1883, by using branches of *Tradescantia*, &c., cut longitudinally, was able[1] to see movements of water and air-bubbles in the vessels and tracheides exposed and placed under the microscope. On stopping up the vessels, the leaves still acting, air-bubbles appeared and grew larger; on removing the leaves the movements ceased: any slight bend, pressure, change of atmospheric moisture, light, &c., had its effect on the movements.

Similar observations were also made in 1883 by Capus,[2] who used *begonias*, *dahlias*, &c., and examined the vessels exposed on sections. The method was to remove a slice so as to expose the

[1] Vesque, "Observations directe du mouvement de l'eau dans les vaisseaux." *Ann. d. Sc. Nat.* Ser. vi. t. xv. 1833, No. 1.

[2] "Sur l'observation directe du mouvement de l'eau dans les plantes." *Comptes Rend.*, 1883, t. 97, p. 1087.

vessels, &c. and then to cut away the opposite side of the stem down to the pith, thus making the exposed parts translucent. His results coincide with those of Vesque.

In the *Berichte der deutschen botanischen Gesellschaft* for 1883, appeared a criticism by Zimmermann,[1] which must not be passed over. He points out that in spite of the favourable features in the more generally approved theories, which explain the water-movements as taking place in the cavities, and not the walls of the elements, they still sin terribly against the laws of physics. It is quite right, he says, to insist, as Boehm and others do, on the importance of the *chapelet de Jamin* as a stable column, but the conditions in the plant do not allow of capillarity being employed as Boehm and Hartig employ it.

For if we suppose that the intervening membranes of superposed tracheides composing a column of water and air-bubbles, present no resistance, then the column simply resolves itself into a sinuous continuous water column, the axis of which turns aside at the air-bubbles. Such a column is supported by the upper meniscus, and can only be as high as accords with the law of capillarity for the particular tube.

[1] "Zur Kritik der Böhm-Hartigschen Theorie der Wasserbewegung in der Pflanze." *Ber. d. d. bot. ges.* B. i. p. 183.

Now suppose the interpolated membranes to exert just sufficient resistance to filtration to balance the water-column contained in its own cell above it, then, as Hartig assumes, the movement will depend entirely on the differences of pressure in the air-bubbles. If water is removed so as to diminish the pressure of a bubble in a given tracheide, then the bubble next below exerts pressure and drives water up, and so on. Zimmermann comes to the conclusion that on this assumption also the lifting forces alleged are not sufficient for the purpose, and that Hartig's theory also fails to account for the ascent of water up trees more than thirty feet or so high, for he finds that the suction action can only be propagated for ten meters or so along the system.

Attention should be drawn to a second paper by Zimmermann,[1] in which he publishes the results of his experiments with a number of Jamin's chaplets, but since the paper deals more particularly with the purely physical phenomena in the glass tubes, it is hardly necessary to discuss it here : it may be noticed that he obtains some curious results with other liquids than water, however, and there can be no doubt as to the importance of the *chapelet de Jamin* in the plant.

[1] " Ueber die Jamin'ische Kette." *Ber. d. deut. bot. Gesellsch.*, 1883. B. i. p. 384.

But the most important contribution to the discussion in 1883, was Westermaier's paper,[1] in which an entirely new departure was made, in that, for the first time,[2] attention was called to the rôle of the living parenchymatous cells of the wood and medullary rays.

Westermaier accepts Zimmermann's criticism as putting the Boehm-Hartig theory out of court, and forthwith calls attention to the wood-parenchyma and medullary rays as integral parts of the tissues concerned in the ascent of the water. He then puts the question, Can these living cells raise the water osmotically? If so we need no longer be troubled with the resistance of the membranes, or the heights of the columns.

Two points are to be noticed: (1) The living cells of the wood-parenchyma are in communication with the tracheal system by numerous pits; and (2) turgid parenchyma allows water to escape by exfiltration into dead contiguous elements.

It may perhaps be assumed that cells lower down

[1] "Zur Kenntniss der osmotischen Leistungen des lebenden Parenchym's." *Ber. der deut. bot. Gesellsch.* B. i. 1883, p. 371.

[2] This is not strictly accurate, as Knight (*Phil. Trans.* 1801, p. 344) had suggested the co-operation of medullary rays, but of course his points of view were different.

tend to exfiltrate water sooner than those at higher levels in the tree, and this being so we have to consider not only the absorbing or *sucking* action of the parenchyma, but also its exfiltration or *forcing* action.

Employing the pith of *Helianthus*, Westermaier found that in summer the lower parts are filled with liquid only at the periphery, whereas in the upper parts of the stem the whole of the pith is full of sap. A cylinder of this pith more than 50 cm. long, at first flaccid, became turgescent in twenty-four hours when exposed to moisture with its end dipped in water.

In such experiments, it may happen that parts here and there, above the level of the water in which the lower end is placed, become turgescent and stiff, while parts lower down are flaccid—pointing to a stronger osmotic draught in the turgid cells.

Applying this to the case under discussion, we must note the numerous points of contact and communication between the tracheal system on the one hand, and the living, osmotically active cells of the wood-parenchyma and medullary rays, on the other.

The hypothesis which follows depends, firstly, on the keeping up of the *chapelet de Jamin*, by supplies of water from the roots. Secondly it must be assumed that the individual columns of the chaplet

are self-supporting—*i.e.* they must obey the law of capillarity, and remain suspended in the tube. That the chaplets exist is a fact of observation, though we do not know their length.

Now consider the system as simplified in a diagram. Suppose a vessel, in contact with medullary rays and wood-parenchyma at different levels. Water rises in the vessel to a given height, the level of the first medullary ray, and is held there by the pressure from below. The parenchyma at that level then uses this water as a store from which it draws by endosmose.

At a somewhat higher level, and in contact with the same vessel, is another medullary ray, the cells of which are wanting in water: they take water by endosmose from parenchyma-cells lower down in the wood, the action reaching to the medullary ray first considered. This absorbent action goes on till these cells of the higher medullary ray also are turgid, and so rich in water that they exfiltrate it into the neighbouring vessel, where the air is rarefied. Here—*i.e.* at a higher level—the expressed water collects into a small column, *growing in both directions upwards and downwards.* This will be supported by capillarity until it reaches a certain length, and before it exceeds this the action will have

been repeated with respect to a medullary ray yet higher up.

We thus have two sets of forces, capillarity and osmosis, supplementing one another: the capillarity only *supports* the columns, the *moving* force is endosmose.

Westermaier points to a sentence in Nägeli and Schwendener's book on the microscope, as having anticipated the probable necessity for distributing the lifting forces at numerous points; and he also claims that his views are supported by their falling in so well with the facts of anatomy.

In contrast to the "Imbibition-" and the "Gas-pressure" theories, the above may be named (the translation is not very happy, I fear) the "climbing" or "clambering" theory.[1]

As regards the bearing of this explanation on Dufour's experiments, the author points out that the continuity of neither the medullary rays nor the obliquely running wood-parenchyma strands, would be broken by the bending or sawing.

Westermaier then puts forward the result of some experiments to measure the hydrostatic pressure and endosmotic power of such cells as enter into considera-

[1] "*Kletterbewegung*"—perhaps "Step-theory" would meet the requirement of the case?

tion here. The principle involved was to oppose pressure, by means of weights, to the resistance due to turgidity, and he came to the conclusion that the hydrostatic pressure concerned may easily reach three and four atmospheres.

The year 1884 saw the publication of several papers on our subject, and one of these seems to have practically closed the discussion except as regards details. I propose to take first one by Elfving,[1] because it introduces some excellent criticisms on the foregoing papers, as well as offering a survey of several physical principles which had been either neglected or not properly understood by previous writers.

Elfving first gives a short summary of the older views, with especial reference to the capillary theory and the bearing of his own previous experiments, and then proceeds to point out that the two sets of forces, *capillarity* which is effective in the lumina of the tracheides and vessels, and *imbibition* in the solid substance of their walls, together with the osmotic forces concerned in root-pressure, and the expansion and contraction of the air bubbles, must all be active in causing the movement of the water up the stem of the tree.

[1] "Ueber den Transpirationsstrom in den Pflanzen." *Acta Societatis Scientiarum Fennicæ*, t. xiv. 1884.

Capillarity and the friction of the air bubbles must be important, as supporting the columns of water.

Imbibition (in Sachs' sense) will be useful when the lumina of the elements are nearly deprived of water in summer.

Osmosis is active in giving a push from behind especially at certain seasons.

The differences of air-pressure as expressed by the contractions and expansions of the bubbles, must have effect in moving small quantities of water from lumen to lumen.

Elfving then proceeds to show that the "gas-pressure theory" of Hartig is but a development of the air-pressure theory of Boehm, though the only point which remains the same in both is the assumption that the water moves in the lumina.

Water is *always* present in the tracheides according to Hartig, Boehm, Russow and Elfving; though of course this does not itself prove that this water is any other than a reserve supply, as Dufour alleges it to be.

The pressure of the atmosphere could have nothing to do with the matter, because the membranes are impervious to air: if it could, the hypothesis as it stands would be absurd; for a continuous column could only be ten meters high. There is no com-

petent *vis a tergo* in the plant, and the capillaries are not narrow enough for the heights required. Boehm, Hartig and others have tried to show that the water columns are held supported and immovable in the lumina, and hence exert no downward pressure which would cause them to fall: Sachs, and those with him, reply that the capillary forces which hold these columns so fast as to prevent their falling, will, with equal obstinacy, prevent their being moved upwards.

Elfving then examines the well-known and oft-quoted experiment of Th. Hartig. The vertical piece of branch—say yew—consists of series of tracheides each containing water and air, and closed by pit-membranes which are very permeable to water; but this constitutes a *chapelet de Jamin*, the only peculiarity being the intercalation of the extremely permeable membranes at more or less regular heights between the columns of water. In Hartig's experiment then, the vertical rows of tracheides form so many immovable *chapelets de Jamin*, but with liquid communications at the permeable pits: the movement of the water, caused by the weight of a drop placed above, must therefore be in a sinuous course, through the lateral pits, and not confined to the one column. If we take this sinuous course, and examine

it, we find it to consist of parts each bounded above and below by an air-bubble, and Elfving's contention in opposition to Zimmermann's, is that the friction of these bubbles and capillarity completely support these parts.

Calculation shows that if the tracheides measure 0·02 mm. in diameter, and have the same capillary ascension as glass (which of course we do not know) then the capillary ascension would = 1·5 meter—a number amply sufficient for the purpose.

Hence, says Elfving, we may safely assume that each short water-column in the series, between its two air-bubbles, exerts no pressure downwards—it is a weightless segment, so to speak—whence the columns may be maintained at any height likely to come into dispute. As to the origin of the air-bubble there is no difficulty. The tracheides, &c. are cells containing protoplasm and other contents when young, but when the walls are thickened and the bordered pits, &c. completed, the living contents disappear, leaving sap only in the cavities. As water is withdrawn a tendency to form a vacuum is instituted, but this is prevented by vapour, the tension of which increases as the withdrawal of water proceeds. Since the water absorbed into the plant contains air, however, the reduction of pressure causes the sap to part

with its air (it cannot retain in solution so much as it could under a higher pressure) and the air will continue to pass off from the sap so long as the pressure is less than an atmosphere. Hence air-bubbles must be produced when more water is passing off at the leaves than is entering at the roots.

The reply that the water held fast by the air-bubbles proves too much, because it is immovable, is anticipated by the remark that though each column is thus fixed as a whole, the individual particles of water are free to move.

We have already examined Elfving's proofs that the water travels through the lumina, and may at once pass to his conclusions. He points out that the imbibition theory was devised to meet the difficulty that water is carried up several hundred feet in the tallest trees, whence the water (1) must be held by molecular forces, (2) must be easily moved: but the theory of intra-cellular water above stated quite agrees with this. Transpiration at the leaves is supplied by osmotic currents from the extremities of the vascular bundles to the mesophyll: these osmotic currents are feeble, but they set the water in movement, *via* the vascular bundles of the ribs and petiole. As soon as the stream encounters an air-bubble, it bends to one

side, and since the friction between the wood-wall and the water, as well as the resistance to filtration, are almost infinitely small, the water in the columns, supported in the long chains by the air-bubbles, moves. If no more water is being transpired than is absorbed, the air-bubbles themselves do not act in the process; but now suppose more water passes off at the leaf-surfaces than is supplied at the roots. In this case the air-bubbles must expand (explaining Hartig's discovery that the air in the upper parts of the tree is rarer) and a "suction" is started, and propagated downwards, accelerating the flow above, and extending its action—which becomes more and more feeble downwards—till it splits into smaller currents at the roots.

Hence, according to Elfving, the opponents of the imbibition theories are right in saying that (1) the water filters from element to element, and (2) that the tension of the air-bubbles co-operates; but they are wrong in supposing (1) that the pressure of the atmosphere can be effective, or (2) that the tension of the air-bubbles only makes the pit-membranes permeable.

In Dufour's experiments with sawn branches, he ignores the effects of cutting in air—the more rapid the transpiration the more quickly air will pass in and prevent water under pressure from passing through,

owing to the impermeability of the wet membranes for air, and the enormous friction of the air-bubbles.

A paper of some interest at the time was published by Max Scheit[1] early in 1884, in which the author boldly denied that air-bubbles exist in the vessels, &c. during the life of the plant, and surmises that they have entered the sections, &c. at the moment of cutting. He argues that only two modes of entrance are possible for the air—(1) through the stomata, which do not communicate with vessels, and (2) as air dissolved in the water entering at the roots. Von Höhnel and Wiesner had proved that air cannot pass directly into vessels, and we know it will not readily traverse wet membranes—and since water is always to be found in the vessels, &c., their walls are never dry during life.

Scheit argued that any air dissolved in water at the roots would be used before it reached the places where it is said to separate out. He gives some conclusive proofs of the impermeability to air of wet wood: even 80 to 120 cm. of mercury failed to drive air through 2—3 cm. of wood.

He concluded that only water and aqueous vapour

[1] "Die Wasserbewegung im Holze." *Bot. Zeitung*, March, 1884, p. 177.

exist in the cavities of the tracheides, and that the system which has to be examined, consists of fine capillary tubes plunged below into cells which absorb water (root-parenchyma, &c.) and above into cells which give off water by evaporation (mesophyll of the leaf), and accompanied on their course by cells of wood-parenchyma and medullary-rays, the latter supplying the cortex with water. The whole conducting mechanism moreover is surrounded by the cambium. The up-taking and giving off of water is accomplished through the bordered pits, and the capillary system is, as we have seen, impermeable to air. It should also be noted that by far the majority of so-called vessels are really tracheides.

So long as the closing membranes of the bordered pits are not stretched, the tracheide is a closed system: pressure on the membrane results in the passage of water in the direction of the pressure, the membrane returning to its original position elastically and preventing the back-flow. Hence the water which traversed the membrane is held in the capillary space above.

There is, said Scheit, no question of the sum of the pressures of the columns in superposed tracheides, because each column is on the one hand held up by capillarity, and on the other, could only exert pressure

on the walls of the tracheide containing it. The diameter of the tracheides (in *Pinus* = 0·015 to 0·02 mm.) shows they could support columns much longer than they do.

Thus the water in the stem is in long columns, broken at short intervals by valves, reminding us of a hint thrown out long ago by De Candolle and Mongolfier.

To get over the difficulty as regards vessels, Scheit raises doubt as to the continuity of their lumina: in any case he regards the capillary water in them as of the nature of a reserve.

The causes of the water-movement are as follows:— Transpiration tends to exhaust the reservoirs of water; the osmotic pressure in the root drives in the closing membranes of the bordered pits, rendering them permeable. The water thus pressed into the vessels, &c. is at once removed from the action of gravity by means of capillarity; and thus the root-pressure has nothing further to do than press the valves and drive water in. Th. Hartig's experiment with the vertical cut branch shows how little pressure is required to do this, and hence the slightest swaying by the wind may be a co-operating cause of movement.

Scheit then quotes experiments in which he injected branches, &c., cut off under the surface of a liquid, and which completely confirm the negative pressure

discovered by Von Höhnel; but which he thinks prove not that air-bubbles under low pressure exist in the transpiring plant, but the existence of a partial vacuum or space filled with aqueous vapour.

Dufour's experiments are severely criticised. The author agrees with Russow that the lumina of the bent shoots were not completely closed, and asks, with Hartig, how it could have been expected they should be, seeing that so many of the elements have comparatively prominent networks and thickenings projecting into the lumina. As regards the sawn branches, the water passes laterally between the two cuts, traversing the bordered pits.

Scheit also insists that Dufour failed to press water through his branches, because the air got in, and found that it was by no means difficult to press liquids through if the cuts were made under water.

He also offered an improvement on Elfving's experiments, stating that two objections have been made to them. In the first place Elfving removed his branches from the tree, and ran the risk of air entering, and secondly the danger of greasing the cell-walls by the cacao-butter rendered the method objectionable. To obviate the latter of these disadvantages Scheit used gelatine coloured with eosin, and completely confirmed Elfving's results.

In *Pringsheim's Jahrbücher* for 1884 appeared a remarkable and brilliant paper by Emil Godlewski,[1] which placed the whole subject in an entirely new position, and seems to have practically closed the discussion as to principles; the papers subsequently published dealing with particular points only.

The paper opens with a critical examination of the previous theories, especially those of Boehm and Hartig, and the author collects what is proved by investigation so far.

Water and air always exist in the lumina of the tracheides, &c., and the movement takes place in the lumina: the imbibition theory of Sachs may be regarded as overthrown by the subsequent researches of Vesque, Elfving, Russow, Hartig and others.

As to the mechanism of the process, several points have to be examined. All the botanists except Boehm agree that osmosis accounts for the absorption of the water from the soil by the root-hairs, and for movements of water in parenchyma generally: Boehm refers the phenomena to differences of pressure, rejecting other causes for the following reasons:

(1) Osmosis acts so slowly.

(2) The epidermis cells, from which transpiration

[1] "Zur Theorie der Wasserbewegung in den Pflanzen," *Pringsheim's Jahrb. f. Wiss. Bot.* b. XV. h. 4, 1884, pp. 569—630.

takes place, contain no chlorophyll-corpuscles, and therefore cannot produce osmotically active substances.

(3) If osmosis replaces the transpired water why do not plants become filled to overflowing when placed in a damp atmosphere?

(4) Green plants placed in the dark for some time ought to use up all their osmotic substances, and would then droop if placed again in the light, whereas they do not do so.

(5) If the movements of water in transpiring leaves is due to osmosis, then so is that in the stem of those plants which have "parenchymatous wood."

To which Godlewski replies as follows:

(1) Movements due to osmosis are slow, it is true, but the distances traversed are very minute, and the fine network of vascular bundles in the leaf is so arranged that no particle of water need have to traverse more than two or three cells.

(2) If we had to assume that no osmosis could occur except at the spots where osmotically active substances are produced, it would follow that no colourless cells can become turgescent—a conclusion falsified by all we know of the cells of pith, roots, parasites, &c. Moreover, Boehm is wrong in ascribing transpiration so expressly to the epidermis cells: it is the

mesophyll cells which give off so much water, to the lacunæ communicating with the air through stomata.

(3) The excretion of liquid water is a special case, and need not be considered here, as it receives full treatment further on.

(4) This depends on the same assumption as (2), and falls with it.

(5) Very few woods are, like that of the *Papayaceæ*, composed largely of parenchyma, and we are not driven to compare such wood forthwith with mesophyll.

Boehm comes in for criticism no less severe with respect to other matters, for his views demand that the epidermis cells and mesophyll, on the one hand, and the root-hairs and parenchyma of the root on the other, must have their contents under less pressure than the atmosphere—an assumption of course opposed to all we know of the cell, turgescence, and the properties of protoplasm and cell-sap. Moreover, to suppose that the pressure in the epidermis and leaf cells, could ever be less than that in the tracheal elements surely ignores the negative pressure which exists in the wood at times of active transpiration; besides we know from actual observations that the cells of the leaf and root show strong turgescence, at just

those times when according to Boehm their elastic walls should be caving in beneath the atmospheric pressure.

Godlewski agrees that there is much to support Boehm's view that the ascent of the water takes place in the lumina of the tracheal elements, since the negative pressure necessary for his theory actually exists there, as proved by Von Höhnel's and other experiments. But however near to ten meters high the pressure of the atmosphere could raise the water in a shrub (and we must always remember that the pressure of the air in the uppermost tracheides will never fall to 0), Boehm's theory is hopeless when applied to trees.

Moreover, all Boehm's attempts to explain the support of the water columns (by the resistance of septa to filtration downwards, and the friction of the air-bubbles, &c.) break down before the fact that any resistance to movement downwards will apply to movement upwards as well.

Finally, Boehm's hypothesis would contradict the principle of the conservation of energy. For if we suppose his system—columns of water broken by air-bubbles and septa, and plunged below in root parenchyma and above in mesophyll—to be eleven meters high, and suppose the root parenchyma to be a

reservoir of water under the pressure of one atmosphere, and if we then create a vacuum in the mesophyll, it would not work. The water would at length sink till its upper level was about ten meters high, because under no conditions could the atmospheric pressure support a higher column. In fact if Boehm's system would work it would furnish a case of "perpetual motion."

Now take Hartig's theory. It may be said to depend on the following facts. The conducting wood always contains liquid water as well as water of imbibition: the alburnum often has more water in the upper parts than in the lower; whenever the amount of water in the tree diminishes, the air-spaces in the crown enlarge more than those in the stem, especially below. Hence, the pressure of the air is less in the upper parts of the tree. Especially striking are Hartig's results with ringed trees, where some species began to droop when the upper parts of the stem still contained 70 per cent. and more of water: in these cases it cannot be because no water, or too little, was present, that the tree drooped, and the only alternative is that the conditions for driving the water up were absent. As we have seen, Hartig assumes these conditions to be the difference of pressure of the air-bubbles—the ringing lets in air, and the continued

transpiration co-operates in bringing about equal pressure all over.

Hartig and others also practically establish the truth of the view that osmosis is the sole cause of absorption and root-pressure, for the root's activity is increased as the temperature of the soil rises a fact irreconcilable with any notion of pressure at the roots being the cause.

Hartig, as we have seen, ascribes osmotic activity to all the parenchymatous and living cells, and claims for the air-bubbles no other function but that of moving the water from lumen to lumen: he also accepts Theodore Hartig's experiment with the vertical piece of branch, using it to prove how slight a pressure is needed for movement. The water once moved through the closing membrane of the pit, becomes arranged by molecular forces in the new cavity, rising in it by capillarity.

But, Godlewski points out, the experiment with the vertical stick has never been properly explained: each writer in succession has assumed properties for it which it does not possess, and the various proposed explanations have again contradicted the principles of physics.

Suppose a glass tube, one meter long and filled with water; both ends closed by membrane perme-

able to water but not to air. Such a tube held vertical lets no water flow out, because no air can enter through the wet membrane above; but if a drop of water is placed on the upper membrane, it is at once absorbed by the water inside, and a corresponding drop appears on the outside of the lower membrane. But the movement is not due to the weight of the drop—it is caused by the weight of *the whole column in the tube;* the whole weight being now greater than the difference of pressures at the top and bottom of the system.

If the tube is divided up by cross membranes, the only difference is that the resistance of several membranes has to be overcome, and a vertically placed stick of Yew is just such a system, whence Hartig's conclusion was wrong.

But he was still more in error in regarding the experiment as proving anything respecting the lifting of the water—the filtration of the water downwards is a very different matter from a lift upwards. Thus supposing we place a piece of Yew branch, one meter long, vertically into ninety cm. of water: if the pressure of Hartig's drop sufficed to move the column, then the pressure of ninety cm. of water ought to drive a very fountain, which of course it does not.

The real explanation of Theodore Hartig's ex-

periment is that the drop of water is absorbed to replace the partial vacuum caused by the down flow of the whole column, and the phenomenon is opposed to—and not in accordance with—Hartig's and Boehm's theories. The drop, as it sinks through the uppermost membrane causes the concave meniscus in each upper tracheide to become more raised and convex, and therefore, for the moment, it cannot support so much as before.

All that the experiment really proves is that the sum of the resistances to filtration of all the membranes is smaller than the pressure of a column of water as long as the wood used.

After further criticisms, Godlewski decides that every hypothesis which requires no further forces than root-pressure, transpiration, and capillarity, must be cast aside as insufficient ; for root-pressure may sink to o when transpiration is active ; transpiration at most cannot produce a vacuum, and hence cannot lift beyond the pressure of one atmosphere ; and the capillary machinery is not adapted to raise water more than a few meters.

Some other factor must be brought into requisition, and Godlewski, like Westermaier, invokes the aid of the living cells of the wood parenchyma and medullary rays, *which are never absent.* These living cells,

placed at numerous successive levels in the stem, act alternately as suction and force pumps: they absorb water forcibly by osmosis, and they drive it out again (also forcibly) by exfiltration at a higher level.

The chief difficulties which face the hypothesis are those which recur when we try to explain root-pressure, and yet it is certain that the living cells of the root-hairs, and root-epidermis, &c., absorb water from the soil and force it into the axial vessels.

Now the phenomenon of "root-pressure" can be got with pieces of older roots, or even bits of stems put into wet sand; and Hofmeister, Russow, Kraus and others have conjectured that the living cells of the wood must co-operate in producing root-pressure, and it is difficult to see how it can be otherwise in such cases as the above.

The next difficulty is to explain how a cell can thus take up water by endosmose, and then drive it out under pressure; for it is impossible to accept Hofmeister and Sachs's hypothesis that the cells are differently constructed on two opposite sides. Moreover, the apparatus designed by Sachs[1] to explain root-pressure will not work—it contradicts the conservation of energy.

[1] This apparatus is represented in Fig. 213, p. 276, of Sachs's *Lectures on the Physiology of Plants*, English edition.

In root-pressure the water driven up at the cut stock contains a smaller percentage of soluble substances than does the sap in the living cells: this means that energy has been employed in separating the *very dilute solution* in the vessels. Moreover, energy is necessary to overcome the resistance to filtration of the cell-membranes, and this often under the pressure of a column of water. Still more will energy be employed if the cells draw their supply of water from vessels, and drive water into vessels again at a higher level.

Hence no mere mechanism of turgescence by osmosis will account for the phenomena, unless we can show that the sap in the cells becomes more concentrated each time, and denser as we ascend the tree: this is not the case.

We must call in the supply of energy set free by the respiration of the protoplasm, as well as turgescence, as furnishing the forces which overcome resistance to filtration, and which separate water again from the dense sap in the cell. In the turgescence of a cell we have, first, water being absorbed owing to the attraction for it exercised by substances in the sap-vacuole; this continues until the tension of the elastic cell wall and the hydrostatic pressure exerted by the water inside are equal, when the cell is turgid.

The process may continue until the pressure inside causes water to filter out through the wall.

But there are two possible ways by which this exfiltration of the water under pressure might occur. (1) By increasing the force which presses the water out ; or (2) by diminishing the attractive forces which retain the water, and if we can assume a regular periodicity of either one of these, we can explain root-pressure.

As a first possibility, suppose a parenchyma-cell in contact with the water of the soil on the one side, and on the other (with the intermediation of other similarly disposed cells) with a tracheide or vessel. Water is absorbed, and the cell in question becomes turgid. Then suppose one or both the following changes to occur in the cell, due to forces liberated by respiration: (1) the protoplasm as a whole contracts, and (2) the particles nearest the vessel undergo some alteration of position, of such a nature as to permit of filtration. The consequence would be that after the tension due to turgescence had reached a certain stage, the protoplasm by violent contraction drives the water forwards : restitution of the turgid condition would then follow, and the process be repeated, and so on.

As a second possibility, let us suppose that respiration brings about changes in the substances which

attract water—*i.e.* the osmotically active substances—of such a kind that they suddenly become less powerful, and can no longer retain their hold on the water, which is therefore freed and escapes in the direction of least resistance. Then the osmotically powerful substances are restored, attract water, and again lose their hold, and so on periodically.

Now, as Godlewski points out, it has been shown by De Vries that every time certain molecular decompositions occur in the cell, the attraction for water is increased ; and it is extremely probable that periodic changes of the following nature occur in the cell—first, certain molecular combinations are built up which have a definite power of attracting water osmotically : then these molecular complexes undergo explosive decompositions under the influence of respiratory oxidation, the larger number of molecules thus formed having a more powerful osmotic attraction for water. De Vries seems to have established, in fact, that with each splitting of a complex compound into simpler ones, the osmotic power of the cell is increased ; while with each union of simpler into more complex molecules it is lessened : and, again, with every solution of a part of the protoplasm, the osmotic power increases ; the reverse occurring each time an excretion of insoluble substances occurs in the cell-sap.

Now it is allowed universally that in a living cell there must be continually recurring splittings of complex to simple bodies, and re-combinations of simple bodies into complex ones; oxidations of organic molecules to carbon dioxide and water; transformations of soluble into insoluble substances, and so on. Whence we have only to assume a certain regularity or periodicity of these processes to have all that is necessary for the hypothesis.

If this is given, we have at the same time an explanation to account for the facts that the sap from a bleeding stump is more dilute than that in the cells; that the root-pressure is so powerful; that old roots may be made to exhibit root-pressure.[1]

If now we take the case of the Conifers, it also explains in a very simple manner the histological peculiarities of the wood. On a transverse section of the stem of a Conifer, any medullary ray-cell, which is in contact above and below and at both ends with similar cells, has a radial row of tracheides on its flanks, and these tracheides have particularly large and open bordered pits on the sides next the medullary ray-cell, water passing easily from cell to

[1] I would also suggest that it may explain the periodicities observed in the out-flow from a cut stump.

tracheide, and *vice versâ*, through the large permeable closing membrane.

At a given time, any of these tracheides contains air and much water : the cell contains protoplasm and osmotic substances.

Now suppose the medullary ray-cell to absorb water osmotically from the tracheides[1] along its two sides, becoming more and more turgid, and the contents pressing the thin membranes outwards into the cavities of the tracheides : this does not involve any change of pressure of the air-bubbles in the tracheides, for the membrane is pushed in towards the cavity as water is withdrawn.

The turgesence of the medullary ray-cell at length attains a maximum. Then follow the changes which lower the osmotic power of the cell contents, and some of the water is driven out under pressure—simply because the cell contents can no longer retain it. This forcible exfiltration of water will increase the pressure on the air-bubbles in the tracheides whence the water came, and so if in any neighbouring tracheide there is less pressure, part of the water absorbed from, say eight tracheides, will escape into that one. Moreover, since the pits are

[1] There may be eight tracheides or more flanking any one medullary ray-cell.

on the radial walls only, this neighbouring tracheide will be in a certain direction only—i.e. *either above or below the level of the medullary ray-cell concerned.*

But, it results from R. Hartig's researches that the air-pressure *decreases upwards*, whence the momentary increase of pressure in the tracheide just referred to will give the water an elastic jog upwards.

Now suppose that renewed decompositions—molecular splittings, &c.,—again occur in the medullary ray-cell: its osmotic attraction again increases, to repeat the above phenomena, and so on. If the pressures in the various tracheides in contact with the medullary ray-cell differ at any given moment, of course the movements are different, for the same moment, in each.

Another point should be noted. When the bulged-out closing membrane of the pit suddenly flattens as the cell loses water, it tends to cause a partial vacuum in the tracheide concerned; hence it exerts a suction-valve action, and water rushes in from the tracheide below—where the air-pressure is somewhat greater.

If we remember that each medullary ray consists of numerous cells, each of which is in contact with several tracheides; and that the number of medullary rays is very large, it is clear that these small

lifts may amount to a good deal, and account for the ascent of the water in the tallest trees.

Above all, the hypothesis explains in an intelligible manner so many hitherto puzzling facts. Thus it explains why, on cutting through the alburnum of a Conifer, the young shoots drooped although 60% of the cubic contents of the tracheides consisted of water. The air-pressure in the parts above the cut becomes equalised, and hence there is no reason for the ascent of the water, but on the contrary every reason for its descent, for the suction will act downwards from tracheide to tracheide, much as in Th. Hartig's experiment.

Again, the hypothesis affords satisfactory explanations of the details of histological structure—*e.g.*, the typical bordered pits are so many funnels and filters: the border is the funnel, the membrane the filter, and the torus acts the parts of the platinum cone used to prevent rupture of the filter, the torus fitting tight into the small hole when the pressure becomes too great. The position of the pits, again, is explained: those tracheides which stand on any one radial row are practically at the same level, whereas those on the next radial row will be a little higher up or lower down —hence water is pressed up step by step and spirally round the stem.

Less obvious, but important, points are the radial elongation of the medullary ray-cell, in order to cover several tracheides—the fine air-canals which run between the cortical and medullary ray-cells, and thus lead from the lenticels—the simple pits which enable the cells of medullary rays to communicate with these air-channels and with one another, and so on.

Godlewski then passes to the consideration of Westermaier's theory of "clambering," pointing out that however similar they may appear, the two views differ greatly in detail.

In the first place Westermaier regards the wood-parenchyma as furnishing the *path* for the movement, as well as the moving forces. He also makes no use of transpiration, and his view would only account for very slow movements; moreover the hypothesis would not apply to the Pines and Firs.

As regards Scheit's views, Godlewski points out that he stands alone in denying (without proving) that no air exists in the tracheal elements: as pointed out over and over again, the water passing in at the roots has air dissolved in it, and even if all else is used up there will be nitrogen gas in the bubbles.

In 1885, Kohl published the results of some experiments[1] bearing on Dufour's statements. He showed

[1] "Zur Wasserleitungsfrage," *Bot. Zeit.* 1885, p. 522.

that when branches are sharply bent, the vessels, if large and few, are compressed like suddenly bent caoutchouc tubes, but although the sectional area is enormously reduced, the lumen of the vessel is not necessarily closed. Moreover, in the notching experiments, with branches sawn half through, it is quite a mistake to suppose that the continuity of the water current is broken; and by squeezing branches in a vice it can be shown that the rapidity of the diminished water-flow may be lessened or increased as the sectional area of the vessels is reduced or enlarged—by screwing up or loosening the grip.

Kohl used branches cut under water, as well as completely rooted plants. He measured the rate of transpiration in the normal condition, and then squeezed the stem in the vice: then, taking numerous readings, he compared the time it took to transpire so much water. It was found possible to screw the vice up tight enough to stop the flow altogether.

Meanwhile a large series of very careful measurements had been and were being made by Fr. Darwin and W. Phillips of Cambridge,[1] of the rate of the transpiration flow under various conditions. Using

[1] "On the Transpiration-stream in Cut Branches," *Proc. Camb. Phil. Soc.* vol. v. pt. v., Nov., 1885, pp. 330-367. See also *Nature*, May 1, 1884.

an air-bubble as indicator, the length of time which it took to traverse a given length of tube measured the rate of flow of the column of water attached to the cut branch. These results are quite independent of Kohl's, and nevertheless bear out the same conclusions, but much more exactly and in detail. The authors show that Dufour (1) was wrong in his estimate of the great obstruction to transpiration produced by the double-sawing, and (2) exaggerated the difficulty of forcing water through doubly-sawn branches.

A single cut produces far less diminution of the rate of flow, than the double cuts. Moreover, the obstruction is greater at first than later on—a recovery of the rate of flow occurs to some extent as the absorbing power in the leaves makes itself felt more and more.

I must refer the reader to the original for further details, merely pointing out that the results are distinctly in favour of the theory that the water passes through the cavities of the vessels and tracheides, and they are the more valuable because low pressures and actual transpiration were employed.

An interesting test of the validity of Godlewski's theory was devised by Janse,[1] who set himself to ask—

[1] "En experimenteel bewys voor de theorie van Godlewski omtreut de bewegung van het water in de planten," *Maand. blad voor Natuur-*

Is the water current arrested or slowed when the living cells of the wood-parenchyma and medullary rays are killed for a distance up the stem? If so we have a strong argument in support of Godlewski's theory.

He accordingly killed all the living cells in a given stretch of a normal branch by running hot water round the latter while still attached to the tree and provided with its foliage.

After killing regions 15 to 20 cm. long by heating them to 70° C for an hour, it was found that the leaves above the tortured portion began to droop (in the case of *Fuchsia globosa*) next day, and were all dead and withered in five days. *Syringa vulgaris* took longer to die, but the final result was the same.

That this was due to the killing of the cells by the hot water was concluded from the observation that control plants remained fresh for a much longer time, even when the whole of the cortex was removed over the same stretch of branch.

Hence Janse concluded that the medullary ray-cells and the wood-parenchyma—living, active cells—

wetek Schappen, 1885, pp. 11–24; *Bot. Zeit.* 1885, p. 302. See also "Die Mitwirkung der Markstrahlen bei der Wasserbewegung im Holze," *Pringsheim's Jahrbücher f. wiss. Bot.* 1887, p. 1–69. And Weber, "Ueber den Einfluss höherer Temperaturen auf die Fahigkeit des Holzes den Transpirationsstrom zu leiten," *Ber. d. d. bot. Gesellsch.* 1885, pp. 345–371.

are indispensable for the ascent of the water in the wood.

In 1886 Leo Errera opened up once more the question of Elfving's experiments,[1] and their critics, and disposed of the latter by using gelatine (as Scheit had done) to stop up the cavities of the elements, and by employing the transpiration-current itself—*i.e.* using cut branches with their foliage on. Hence he confuted the objection that Elfving had only proved the case for filtration under pressures.

Branches were used (1) cut under water, so as to inject the vessels with water; (2) cut in air, and the vessels therefore largely filled with air; (3) cut under liquid gelatine, so as to stop up the lumina when the gelatine congealed. The surfaces were then cut clean, and the three sets of branches, in water, exposed to transpiration.

It was found that those blocked with gelatine drooped at once, but recovered if cut higher up; whereas the others transpired normally.

Errera also adds a critical note derived from Sachs's own statements; the latter says,[2] that the thick walled and dense autumnal wood of each

[1] L. Errera, "Ein Transpiration Versuch," *Ber. d. Deutsch. Bot. Gesellsch.*, 1886, p. 16.

[2] *Vorles. über p. Physiologie*, p. 275.

annual ring is less capable of conducting water than the large-celled spring-wood of the same ring; and Errera implies that this is hardly what one would expect if the imbibition theory were true.

Notwithstanding the obvious tendency of the criticisms given in the above, and previous papers, however, Sachs published a second edition of his *Vorlesungen* in 1887, in which he maintains his original position, and scarcely notices any of the difficulties which have been raised since 1882. The note on p. 225-226 can scarcely be regarded as a reply to what has been urged by Elfving, Hartig, Westermaier, Godlewski, and others, and it must be accepted that the great botanist has nothing further to add in support of his original hypothesis.[1]

We must therefore judge between the two prominent theories—the imbibition theory of Sachs, and the osmosis-gas-pressure theory of Hartig and

[1] The reader who is interested in further criticism on details should consult the following memoirs: Zimmermann, "Zur Godlewskischen Theorie der Wasserbewegung in der Pflanzen," *Ber. d. d. bot. Gesellsch.* 1885, pp. 290–292. Hansen, "Ein Beitrag zur Kenntniss des Transpirationsstromes," *Arb. d. bot. Inst. Würsburg*, 1885, pp. 305–314. Scheit, "Die Wasserbewegung im Holze," *Jenaische Zeitschrift fur Naturk*, 1885, pp. 678–734. Schwendener, "Untersuchimgen ueber das Saftsteigen," *Sitzungsber. d. k. preuss. Akad. d. Wiss.* 1886, pp. 561–602. Scheit, "Beitrag zur Widerlegung der Imbibitionstheorie," *Jenaische Zietschr.* 1885.

Godlewski, and others—by applying the usual test in inductive science. Which explains most facts? On the one hand we have the daring assumption of Sachs, transcending experience, and, indeed, apparently incapable of being tested: if we accept it, we shut our eyes to the facts of the anatomy of wood almost entirely; the medullary-rays, the bordered pits, the presence of air-bubbles in the tracheides, and even the existence of the tracheides, with numerous other structural peculiarities become mere anomalies.

On the other hand Hartig and Godlewski's improved osmosis-pressure theory gives us an intelligible explanation for all the above, and many other phenomena; and even if it be urged that Godlewski takes refuge at last in the respiration of protoplasm to furnish his lifting forces, and that the rhythmical periodicity in this process necessary for his theory is not proved—even granting all this, I think it is important to note that Godlewski carries the whole question many steps forward before he has to appeal to his assumed periodicity. Moreover, it has also to be admitted that recent researches are in favour of Godlewski's views as to the behaviour of the protoplasm.

In conclusion, it seems fair to think that the present

position of the controversy is a satisfactory result of the labours that have been expended on the question, for although it may be urged that we have no idea as to the *modus operandi* in the actual lifting process, and that, in common with so many other physiological processes, the whole phenomenon is thrown back to that limbo of biology, "the properties of protoplasm," nevertheless the physiologist has had numerous new questions put into new lights for him, the anatomist and histologist have been driven to find out more facts, and the physicist and chemist have been stimulated by the controversy into examining new and more complex forms of apparatus. Moreover, it may be fairly said in reply to those who cavil at the results, that the loss of mental satisfaction involved in the last resort to the respiration of living protoplasm as furnishing the lifting forces, is by no means greater than that implied in a complacent acceptance of Sachs's transcendental hypothesis, which cuts the knot by assuming properties of the cell-walls and their imbibed water which apparently cannot be tested.

I should also like to suggest that the hypothesis of periodicity of respiration, implied in the modern theories, seems by no means inconsistent with many known phenomena—*e.g.* periodic irritable movements,

periodic growth, the periodicity seen in the well-known phenomena due to root-pressure, and in many other cases—and would venture to point out that perhaps some of the grandest results in biology may be looked for along the lines of research which shall unravel the problem of these phenomena of periodicity. Of course, in a certain sense it is to be expected that a given mass of protoplasm will offer, at the boundary between its own substance and that of the environment, a limited quantity of combustible material; and it is easy to argue that when this has been consumed a pause must ensue—a pause of weariness, exhaustion, on the one hand, and for restitution, refreshment, on the other. Possibly something of the kind is seen in every *Amœba* with a contractile vacuole, and in every growing *Spirogyra* cell. But the time seems to be approaching when it may be possible to generalise with respect to the larger rhythmical periods depending on co-ordination of these, and Godlewski's suggestions, taken in common with those of De Vries, Pfeffer, and other recent workers, seem to point to periodicity in the changes going on in protoplasm, as a grand problem for solution.

CHAPTER V.

DISEASES OF TIMBER.

Trametes radiciperda.

HAVING now obtained some idea of the principal points in the structure, functions, and varieties of normal healthy timber, we may pass to the consideration of some of the diseases which affect it. The subject seems to fall very naturally into two convenient divisions, if we agree to treat of (1) those diseases which make their appearance in the living trees, and (2) those which are only found to affect dead timber after it is felled and sawn up. In reality, however, this mode of dividing the subject is purely arbitrary, and the two categories of diseases are linked together by all possible gradations.

Confining our attention for the present to the diseases of standing timber—*i.e.* which affect

undoubtedly living trees—it can soon be shown that they are very numerous and varied in kind; hence it will be necessary to make some choice of what can best be described here. I shall therefore propose for the present to leave out of account those diseases which do injury to timber indirectly, such as leaf-diseases, the diseases of buds, growing roots, and so forth, as well as those which do harm in anticipation by injuring or destroying seedlings and young plants. The present chapter will thus be devoted to some of the diseases which attack the timber in the trees which are still standing; and as those caused by fungus parasites are the most interesting, we will confine our attention to them.

It has long been known to planters and foresters that trees become rotten at the core, and even hollow, at all ages and in all kinds of situations, and that in many cases the first obvious signs that anything is the matter with the timber make their appearance when, after a high gale, a large limb snaps off, and the wood is found to be decayed internally. Now it is by no means implied that this rotting at the core—"wet-rot," "red-rot," &c., are other names generally applied to what is really a class of diseases—is *always* referable to a single cause; but it is certain that in a large number of cases it is due to the ravages of

fungus parasites. The chief reason for popular misconceptions regarding these points is want of accurate knowledge of the structure and functions of wood on the one hand, and of the nature and biology of fungi on the other. The words disease, parasitism, decomposition, &c., convey very little meaning unless the student has had opportunities of obtaining some such knowledge of the biology of plants as can only be got in a modern laboratory: under this disadvantage the reader may not always grasp the full significance of what follows, but it will be at least clear that such fungi demand attention as serious enemies of our timber.

It will be advantageous to illustrate the remarks I have to make by a description of one or two of the contents of what is perhaps one of the most instructive and remarkable museums in the world—the Museum of Forest Botany in Münich, which I have lately had the good fortune to examine under the guidance of Prof. Robert Hartig, the distinguished botanist to whose energy the Museum is due, and to whose brilliant investigations we owe nearly all that has been discovered of the diseases of trees caused by the Hymenomycetes. Not only is Prof. Hartig's collection unique in itself, but the objects are classical, and illustrate facts which are as yet hardly

known outside the small circle of specialists who have devoted themselves to such studies as are here referred to.

One of the most disastrous of the fungi which attack living trees is *Trametes radiciperda* (Hartig) the *Polyporus annosus* of Fries, and it is especially destructive to the Conifers. Almost every one is familiar with some of our common Polyporei, especially those the fructifications of which project like irregular brackets of various colours from dead stumps, or from the stems of moribund trees ; well, such forms will be found on examination to have numerous minute pores on the under side or on the upper side of their cheese-like, corky, or woody substance, and the spores which reproduce the fungus are developed on the walls lining these many pores, to which these fungi owe their name. *Trametes radiciperda* is one of those forms which has its pores on the upper side of the spore-bearing fructification, and presents the remarkable peculiarity of developing the latter on the exterior of roots beneath the surface of the soil (Fig. 11).

This is not the place to discuss the characters of species and genera, nor to enter in detail into the structure of fungi, but it is necessary to point out that in those cases where the casual observer sees

FIG. 11.—Portion of root of a spruce-fir, with fructification of *Trametes radiciperda* (after Hartig). Each fructification is a yellowish-white mass of felt-like substance spread over the root, and with minute pores, in which the spores are produced, on its outer surface; the mycelium which has developed it is in the interior of the root.

only the fructification of a Polyporus, or of a toad-stool, or of a mushroom (projecting from a rotting stump or from the ground, for instance), the botanist knows that this fructification is attached to, and has taken origin from, a number of fine colourless filaments woven into a felt-like mass known as the mycelium, and that this felt-work of mycelium is spreading on and in the rotten wood, or soil, or whatever else the fungus grows on, and acts as roots, &c., for the benefit of the fructification.

Now, the peculiarity of the mycelium of this *Trametes radiciperda* is that it spreads in the wood of the roots and trunks of pines and firs and other Conifers, and takes its nourishment from the wood-substance, &c., and it is principally to the researches of Hartig that we owe our knowledge of how it gets there and what it does when there. He found that the spores germinate easily in the moisture around the roots, and put forth filaments which enter between the bark-scales, and thus the mycelium establishes itself in the living tree, between the cortex and the wood (Fig. 12). It is curious to note that the spores may be carried from place to place by mice and other burrowing animals, since this Trametes is apt to develop its fructification and spores in the burrows, and they are rubbed off into the fur of the

animals as they pass over and under the spore-bearing mass.

When the mycelium obtains a hold in the root, it

FIG. 12.—Piece of root of spruce-fir, with the mycelium of *Trametes radiciperda* (after Hartig) enlarged about 3 times. The white mycelium spreads in a fan-like manner over the surface beneath the cortex, as seen in the figure where the latter has been lifted and removed (*a*). Here and there the mycelium bursts through the cortex in the form of white protuberances (*b*), to form the fructifications.

soon spreads between the cortex and the wood, feeding upon, and of course destroying, the cambium.

Here it spreads in the form of thin flattened bands, with a silky lustre, making its way up the root to the base of the stem, whence it goes on spreading further up into the trunk (Fig. 12).

Even if the mycelium confined its ravages to the cambial region, it is obvious, from what was described in Chapters I. and II., that it would be disastrous to the tree; but its destructive influence extends much further than this. In the first place, it can spread to another root belonging to another tree, if the latter comes in contact in the moist soil with a root already infected; in the second place, the mycelium sends fine filaments in all directions into the wood itself, and the destructive action of these filaments—called hyphæ—soon reduces the timber, for several yards up the trunk, to a rotting, useless mass. After thus destroying the roots and lower parts of the tree, the mycelium may then begin to break through the dead bark, and again form the fructifications referred to.

Since, as we shall see, *Trametes radiciperda* is not the only fungus which brings about the destruction of standing timber from the roots upwards, it may be well to see what characters enable us to distinguish the disease thus induced, in the absence of the fructification.

The most obvious external symptoms of the disease

in a plantation, &c., are: the leaves turn pale, and then yellow, and die off; then the lower part of the stem begins to die, and rots, though the bark higher up may preserve its normal appearance. If the bark is removed from one of the diseased roots or stems, there may be seen the flat, silky, white bands of mycelium running in the plane of the cambium, and here and there protruding tiny white cushions between the scales of the bark (Fig. 12); in advanced stages the fructifications developed from these cushions may also be found. The wood inside the diseased root will be soft and damp, and in a more or less advanced stage of decomposition.

On examining the timber itself, we again obtain distinctive characters which enable the expert to detect the disease at a glance. I had the good fortune some time ago to spend several pleasant hours in the Münich Museum examining and comparing the various diseases of timbers, and it is astonishing how well marked the symptoms are. In the present case the wood at a certain stage presents the appearance represented in the drawing, Fig. 13. The general tone is yellow, passing into a browner hue. Scattered here and there in this ground-work of still sounder wood are peculiar oval or irregular patches of snowy white, and in the centre of each white patch is a black speck. Nothing

surprised me more than the accuracy with which Prof. Hartig's figures reproduce the characteristic appearance of the original specimens in his classical collection,

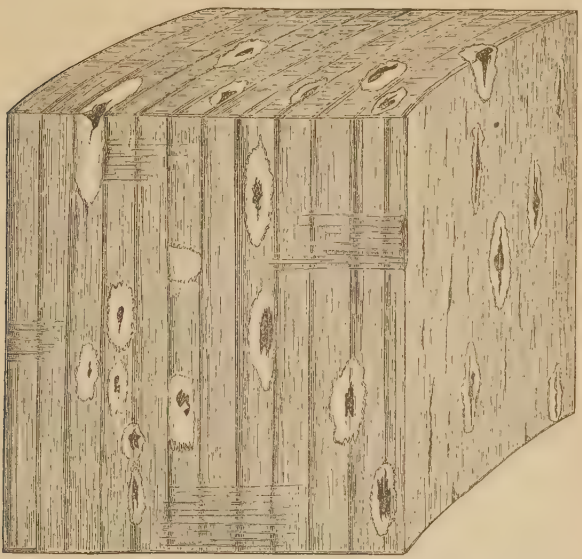

FIG. 13.—A block of the timber of a spruce-fir, attacked by *Trametes radiciperda*. The general colour is yellow, and in the yellow matrix of less rotten wood are soft white patches, each with a black speck in it. These patches are portions completely disorganized by the action of the mycelium, and the appearance is very characteristic of this particular disease. (After Hartig.)

and I have tried to copy this in the woodcut, but of course the want of colour makes itself evident.

It is interesting and important to trace the earlier changes in the diseased timber. When the filaments

of the fungus first begin to enter the wood, they grow upwards more rapidly than across the grain, piercing the walls of the cells and tracheides by means of a secretion—a soluble ferment—which they exude. This ferment softens and dissolves the substance of the walls, and therefore, of course, destroys the structure and firmness, &c., of the timber. Supposing the filaments to enter cells which still contain protoplasm and starch, and other nutritive substances (such as occur in the medullary rays, for example), the filaments kill the living contents and feed on them. The result is that what remains unconsumed acquires a darker colour, and this makes itself visible in the mass to the unaided eye as a rosy or purple hue, gradually spreading through the attacked timber. As the destructive action of the fungus proceeds in the wood, the purple shades are gradually replaced by a yellowish cast, and a series of minute black dots make their appearance here and there, then the black dots gradually surround themselves with the white areas, and we have the stage shown in Fig. 13.

These white areas are the remains of the elements of the wood which have already been completely delignified by the action of the ferment secreted by the fungus filaments—*i.e.* the hard woody cell-walls have become converted into soft and swelling cellulose,

and the filaments are dissolving and feeding upon the latter (Fig. 14). In the next stage of the advancing

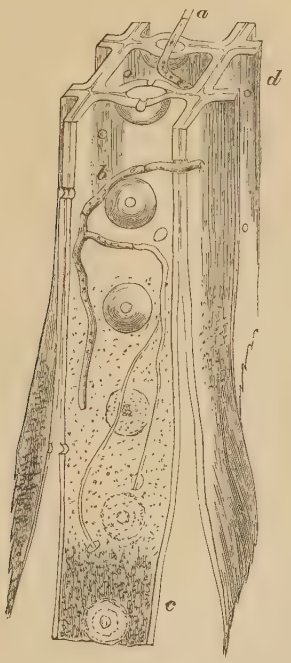

FIG. 14.—Sectional view of a tracheide of the spruce-fir, attacked by the hyphæ (*a*, *b*) of a *Trametes*, highly magnified (after Hartig). The upper part of the tracheide has its walls still sound, though already pierced by the hyphæ; the lower part (*c*) has the walls completely delignified, and converted into cellulose, which swells up and dissolves. The middle-lamella is also undergoing dissolution. The holes in the walls have been bored by hyphæ.

destruction of the timber the black dots mostly disappear, and the white areas get larger; the middle-

lamella between the contiguous elements of the wood subsequently dissolves, and soft places and cavities are produced, causing the previously firm timber to become spongy and soft, and it eventually breaks up into a rotting mass of vegetable remains.

It will readily be understood that all these progressive changes are accompanied by a decrease in the specific gravity of the timber, for the fungus decomposes the substance much in the same way as it is decomposed by putrefaction or combustion, *i.e.* it causes the burning off of the carbon, hydrogen, and nitrogen, in the presence of oxygen, to carbon-dioxide, water, and ammonia, retaining part in its own substance for the time being, and living at its expense.

CHAPTER VI.

DISEASES DUE TO *AGARICUS MELLEUS* AND *POLYPORUS SULPHUREUS*.

BEFORE proceeding further it will be of advantage to describe another tree-killing fungus, which has long been well known to mycologists as one of the commonest of our toadstools growing from rotten stumps, and decaying wood-work such as old water-pipes, bridges, &c. This is *Agaricus melleus* (Fig. 15), a tawny yellow toadstool with a ring round its stem, and its gills running down on the stem and bearing white spores, and which springs in tufts from the base of dead and dying trees during September and October. It is very common in this country, and I have often found it on beeches and other trees in Surrey, but it has been regarded as simply springing from the dead rotten wood, &c., at the base of the tree. As a matter of fact, however, this toadstool is traced to a

series of dark shining strings, looking almost like the purple-black leaf-stalks of the maidenhair fern, and

FIG. 15.—A small group of *Agaricus* (*Armillaria*) *mellens*. The toad-stool is tawny-yellow, and produces white spores; the gills are decurrent, and the stem bears a ring. The fine hair-like appendages on the pileus should be bolder.

these strings branch and meander in the wood of the tree, and in the soil, and may attain even great

lengths—several feet, for instance. The interest of all this is enhanced when we know that until the last few years these long black cords were supposed to be a peculiar form of fungus, and were known as *Rhizomorpha.* They are, however, the subterranean vegetative parts (mycelium) of the Agaric we are concerned with, and they can be traced without break of continuity from the base of the toadstool into the soil and tree (Fig. 16). I have several times followed these dark mycelial cords into the timber of old beeches and spruce-fir stumps, but they are also to be found in oaks, plums, various Conifers, and probably may occur in most of our timber-trees if opportunity offers.

The most important point in this connection is that *Agaricus melleus* becomes in these cases a true parasite, producing fatal disease in the attacked timber-trees, and, as Hartig has conclusively proved, spreading from one tree to another by means of the rhizomorphs underground. In the summer of 1887 I had an opportunity of witnessing, on a large scale, the damage that can be done to timber by this fungus. Hundreds of spruce-firs with fine tall stems, growing on the hill sides of a valley in the Bavarian Alps, were shown to me as "victims to a kind of rot." In most cases the trees (which at first sight appeared only

slightly unhealthy) gave a hollow sound when struck, and the foresters told me that nearly every tree was rotten at the core. I had found the mycelium of

FIG. 16.—Sketch of the base of a young tree (*s*), killed by *Agaricus melleus*, which has attacked the roots, and developed rhizomorphs at *r*, and fructifications. To the right the fructifications have been traced by dissection to the rhizomorph strands which produced them.

Agaricus melleus in the rotting stumps of previously felled trees all up and down the same valley, but it was not satisfactory to simple assume that the "rot"

was the same in both cases, though the foresters assured me it was so.

By the kindness of the forest manager I was allowed to fell one of these trees. It was chosen at hazard, after the men had struck a large number, to show me how easily the hollow trees could be detected by the sound. The tree was felled by sawing close to the roots: the interior was hollow for several feet up the stem, and two of the main roots were hollow as far as we could poke canes, and no doubt further. The dark-coloured rotting mass around the hollow was wet and spongy, and consisted of disintegrated wood held together by a mesh-work of the rhizomorphs. Further outwards the wood was yellow, with white patches scattered in the yellow matrix, and, again, the rhizomorph-strands were seen running in all directions through the mass.

Not to follow this particular case further—since we are concerned with the general features of the diseases of timber—I may pass to the consideration of the diagnosis of this disease caused by *Agaricus melleus*, as contrasted with that due to *Trametes radiciperda*.

Of course no botanist would confound the fructification of the *Trametes* with that of the *Agaricus;* but the fructifications of such fungi only appear at certain seasons, and that of *Trametes radiciperda* may

be underground, and it is important to be able to distinguish such forms in the absence of the fructifications.

The external symptoms of the disease, where young trees are concerned, are similar in both cases. In a plantation at Freising, in Bavaria, I have been shown young Weymouth pines (*P. Strobus*) attacked and killed by *Agaricus melleus*. The leaves turn pale and yellow, and the lower part of the stem—the so-called "collar"—begins to die and rot, the cortex above still looking healthy. So far the symptoms might be those due to the destructive action of other forms of tree-killing fungi.

On uprooting a young pine, killed or badly attacked by the Agaric, the roots are found to be matted together with a ball of earth permeated by the resin which has flowed out: this is very pronounced in the case of some pines, less so in others. On lifting up the scales of the bark, there will be found, not the silky, white, delicate mycelium of the *Trametes*, but probably the dark cord-like rhizomorphs: there may also be flat white rhizomorphs in the young stages, but they are easily distinguished. These dark rhizomorphs may also be found spreading around into the soil from the roots, and indeed they look so much like thin roots that we can at once understand their

name—rhizomorph. The presence of the rhizomorphs and (in the case of the resinous pines) the outflow of resin and sticking together of soil and roots are good distinctive features. No less evident are the differences to be found on examining the diseased timber, as exemplified by Prof. Hartig's magnificent specimens. The wood attacked assumes brown and bright yellow colours, and is marked by sharp brown or nearly black lines, bounding areas of one colour and separating them from areas of another colour. In some cases the yellow colour is quite bright—canary yellow, or nearly so. The white areas scattered in this yellow matrix have no black specks in them, and can thus be distinguished from those due to the *Trametes*. In advanced stages the purple-black rhizomorphs will be found in the soft, spongy wood.

The great danger of *Agaricus melleus* is its power of extending itself beneath the soil by means of the spreading rhizomorphs: these are known to reach lengths of several feet, and to pass from root to root, keeping a more or less horizontal course at a depth of 6 or 8 inches or so in the ground. On reaching the root of another tree, the tips of the branched rhizomorph penetrate the living cortex, and grow forward in the plane of the cambium, sending off smaller ramifications into the medullary rays and (in the case

of the pines, &c.) into the resin passages. The hyphæ of the ultimate twigs enter the tracheides, vessels, &c., of the wood, and delignify them, with changes of colour and substance as described. Reference must be made to Prof. Hartig's publications for the details which serve to distinguish histologically between timber attacked by *Agaricus melleus* and by *Trametes* or other fungi. Enough has been said to show that diagnosis is possible, and indeed, to an expert, not difficult.

It is at least clear from the above sketch that we can distinguish these two kinds of diseases of timber, and it will be seen on reflection that this depends on knowledge of the structure and functions of the timber and cambium on the one hand, and proper acquaintance with the biology of the fungi on the other. It is the victory of the fungus over the timber in the struggle for existence which brings about the disease; and one who is ignorant of these points will be apt to go astray in any reasoning which concerns the whole question. Any one knowing the facts and understanding their bearings, on the contrary, possesses the key to a reasonable treatment of the timber; and this is important, because the two diseases referred to can be eradicated from young plantations, and the areas of their ravages limited in older forests.

Suppose, for example, a plantation presents the following case. A tree is found to turn sickly and die, with the symptoms described, and trees immediately surrounding it are turning yellow. The first tree is at once cut down, and its roots and timber examined, and the diagnosis shows the presence of *Agaricus melleus* or of *Trametes radiciperda*, as the case may be. Knowing this, the expert also knows more. If the timber is being destroyed by the *Trametes*, he knows that the ravaging agent can travel from tree to tree by means of roots in contact, and he at once cuts a ditch around the diseased area, taking care to include the recently-infected and neighbouring trees. Then the diseased timber is cut, because it will get worse the longer it stands, and the diseased parts burnt. If *Agaricus melleus* is the destroying agent, a similar procedure is necessary ; but regard must be had to the much more extensive wanderings of the rhizomorphs in the soil, and it may be imperative to cut the moat round more of the neighbouring trees. Nevertheless, it has also to be remembered that the rhizomorphs run not far below the surface. However, my purpose here is not to treat this subject in detail, but to indicate the lines along which practical application of the truths of botanical science may be looked for. The reader who wishes to go further into the subject may

consult special works. Of course the spores are a source of danger, but need be by no means so much so where knowledge is intelligently applied in removing young fructifications.

I will now pass on to a few remarks on a class of disease-producing timber fungi which present certain peculiarities in their biology. The two fungi which have been described are true parasites, attacking the roots of living trees, and causing disease in the timber by travelling up the cambium, &c., into the stem: the fungi I am about to refer to are termed wound-parasites, because they attack the timber and trees at the surfaces of wounds, such as cut branches, torn bark, frost-cracks, &c., and spread from thence into the sound timber. When we are reminded how many sources of danger are here open in the shape of wounds, there is no room for wonder that such fungi as these are so widely spread. Squirrels, rats, cattle, &c., nibble or rub off bark; snow and dew break branches; insects bore into stems; wind, hail, &c., injure young parts of trees; and in fact small wounds are formed in such quantities that if the fructifications of such fungi as those referred to are permitted to ripen indiscriminately, the wonder is not that access to the timber is gained, but rather that a tree of any considerable age escapes at all.

One of the commonest of these is *Polyporus sulphureus* (Fig. 17), which does great injury to all kinds of standing timber, especially the oak, poplar, willow, hazel, pear, larch, and others. It is probably well

FIG. 17.—*Polyporus sulphureus*: portion of the fungus springing from a piece of bark. (After Hartig.)

known to most foresters, as its fructification projects horizontally from the diseased trunks as tiers of bracket-shaped bodies of a cheese-like consistency; bright yellow below, where the numerous minute pores are, and orange or somewhat vermilion above, giving

the substance a coral-like appearance. I have often seen it in the neighbourhood of Englefield Green and Windsor, and it is very common in England generally.

If the spore of this *Polyporus* lodges on a wound

FIG. 18.—Piece of timber infested with the mycelium of *P. sulphureus*: the white masses of fungus fill up the rings and rays produced by their "rotting" action. (After Hartig.)

which exposes the cambium and young wood, the filaments grow into the medullary rays and the vessels, and soon spread in all directions in the timber, especially longitudinally, causing the latter to assume

a warm brown colour and to undergo decay. In the infested timber are to be observed radial and other crevices filled with the dense felt-like mycelium formed by the common growth of the innumerable branched

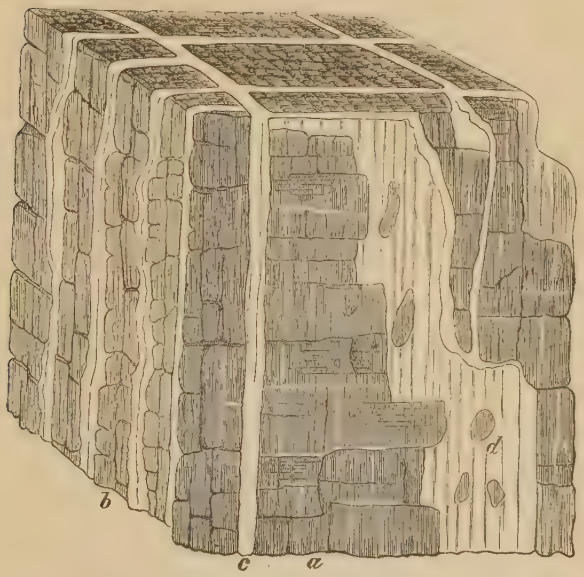

FIG. 19.—Piece of timber completely destroyed by *P. sulphureus*, the mycelium of which fills up the crevices as a white felt. (After Hartig.)

filaments (Figs. 18 and 19). In bad cases it is possible to strip sheets of this yellowish white felt-work out of the cracks, and on looking at the timber more closely (of the oak, for instance) the vessels are found

to be filled with the fungus filaments, and look like long white streaks in longitudinal sections of the wood—showing as white dots in transverse sections.

It is not necessary to dwell on the details of the histology of the diseased timber: the ultimate filaments of the fungus penetrate the walls of all the cells and vessels, dissolve and destroy the starch in the medullary rays, and convert the lignified walls of the wood elements back again into cellulose. This evidently occurs by some solvent action, and is due to a ferment excreted from the fungus filaments, and the destroyed timber becomes reduced to a brown mass of powder.

I cannot leave this subject without referring to a remarkably interesting specimen in the Münich Museum. This is a block of wood containing an enormous irregularly spheroidal mass of the white felted mycelium of this fungus, *Polyporus sulphureus*. The mass has been cut clean across, and the section exposes a number of thin brown ovoid bodies embedded in the closely-woven felt: these bodies are of the size and shape of acorns, but are simply hollow shells filled with the same felt-like mycelium as that in which they are embedded. They are cut in all directions, and so appear as circles in some cases. These bodies are, in fact, the outer shells of so many

acorns, embedded in and hollowed out by the mycelium of *Polyporus sulphureus*. Hartig's ingenious explanation of their presence speaks for itself. A squirrel had stored up the acorns in a hollow in the timber, and had not returned to them—what tragedy intervenes must be left to the imagination. The *Polyporus* had then invaded the hollow, and the acorns, and had dissolved and destroyed the cellular and starchy contents of the latter, leaving only the cuticularized and corky shells, looking exactly like fossil eggs in the matrix. I hardly think geology can beat this for a true story.

The three diseases so far described serve very well as types of a number of others known to be due to the invasion of timber and the dissolution of the walls of its cells, fibres, and vessels by Hymenomycetous fungi, *i.e.* by fungi allied to the toadstools and polypores. They all "rot" the timber by destroying its structure and substance, starting from the cambium and medullary rays.

To mention one or two additional forms, *Trametes Pini* is common on pines, but, unlike its truly parasitic ally, *Tr. radiciperda*, which attacks sound roots, it is a wound-parasite, and seems able to gain access to the timber only if the spores germinate on exposed surfaces. The disease it produces is very like that

caused by its ally: probably none but an expert could distinguish between them, though the differences are clear when the histology is understood.

Polyporus fulvus is remarkable because its hyphæ destroy the middle-lamella, and thus isolate the tracheides in the timber of firs; *Polyporus borealis* also produces disease in the timber of standing Conifers; *Polyporus igniarius* is one of the commonest parasites on trees such as the oak, &c., and produces in them a disease not unlike that due to the last form mentioned; *Polyporus dryadeus* also destroys oaks, and is again remarkable because its hyphæ dissolve the middle-lamella.

With reference to the two fungi last mentioned it will be interesting to describe a specimen in the Museum of Forest Botany in Münich, since it seems to have a possible bearing on a very important question of biology, viz. the action of soluble ferments.

It has already been stated that some of these tree-killing fungi excrete ferments which attack and dissolve starch-grains, and it is well known that starch-grains are stored up in the cells of the medullary rays found in timber. Now, *Polyporus dryadeus* and *P. igniarius* are such fungi; their hyphæ excrete a ferment which completely destroys the starch-grains in the cells of the medullary rays of the oak, a tree very apt to be

attacked by these two parasites, though *P. igniarius*, at any rate, attacks many other dicotyledonous trees as well. It occasionally happens that an oak is attacked by both of these Polyporei, and their mycelia

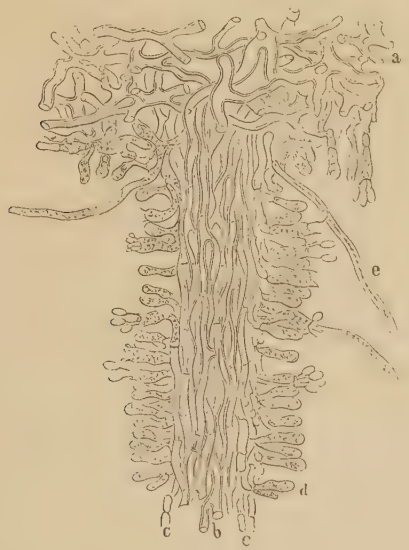

FIG. 20.—Vertical section through the wall of one of the pores of *P. sulphureus*, showing the ordinary hyphæ (*e*), tissue of the fructification (*a* and *b*), and the spore-bearing ends (*d* and above). (After Hartig.)

become intermingled in the timber: when this is the case the *starch-grains remain intact in those cells which are invaded simultaneously by the hyphæ of both fungi.* I have been shown longitudinal radial sections of

oak-timber thus attacked, and the medullary rays of which appeared as glistening white plates. These plates consist of nearly pure starch : the hyphæ have destroyed the cell-walls, but left the starch intact. It is easy to suggest that the two ferments acting together exert (with respect to the starch), a sort of inhibitory action one on the other ; but it is also obvious that this is not the ultimate explanation, and one feels that the matter deserves further investigation.

It now becomes a question—What other types of timber-diseases shall be described ? Of course the limits of a popular book are too narrow for anything approaching an exhaustive treatment of such a subject, and nothing has as yet been said of several other diseases due to crust-like fungi often found on decaying stems, or of others due to certain minute fungi which attack healthy roots. Then there is a class of diseases which commence in the bark or cortex of trees, and extend thence into the cambium and timber : some of these " cankers," as they are often called, are proved to be due to the ravages of fungi, though there is another series of apparently similar " cankers " which are caused by other variations in the environment—the atmosphere and weather generally.

It would need many chapters to place the reader *au courant* with the chief results of what is known of

these diseases, and I must be content here with the bare statement that these "cankers" are in the main due to local injury or destruction of the cambium. If the normal cylindrical sheet of cambium is locally irritated or destroyed, no one can wonder that the thickening layers of wood are not continued normally at the locality in question: the uninjured cells are also influenced, and abnormal cushions of tissue formed which vary in different cases. Now, in "cankers" this is—put shortly—what happens: it may be, and often is, due to the local action of a parasitic fungus; or it may be—and, again, often is—owing to injuries produced by the weather, in the broad sense, and saprophytic organisms may subsequently invade the wounds.

The details as to how the injury thus set up is propagated to other parts—how the "canker" spreads into the bark and wood around—*are* details, and would require considerable space for their description: the chief point here is again the destructive action of mycelia of various fungi, which by means of their powers of pervading the cells and vessels of the wood, and of secreting soluble ferments which break down the structure of the timber, render the latter diseased and unfit for use. The only too well known larch-disease is a case in point; but, since this is a subject

which needs a chapter to itself, I may pass on to more general remarks on what we have learnt so far.

It will be noticed that, whereas such fungi as *Trametes radiciperda* and *Agaricus melleus* are true parasites which can attack the living roots of trees, the other fungi referred to can only reach the interior of the timber from the exposed surfaces of wounds. It has been pointed out along what lines the special treatment of the former diseases must be followed, and it only remains to say of the latter: take care of the cortex and cambium of the tree, and the timber will take care of itself. It is unquestionably true that the diseases due to wound-parasites can be avoided if no open wounds are allowed to exist. Many a fine oak and beech perishes before its time, or its timber becomes diseased and a high wind blows the tree down, because the spores of one of these fungi alight on the cut or torn surface of a pruned or broken branch. Of course it is not always possible to carry out the surgical operations, so to speak, which are necessary to protect a tree which has lost a limb, and in other cases no doubt those responsible have to discuss whether it costs more to perform the operations on a large scale than to risk the timber. With these matters I have nothing to do here, but the fact remains that by properly closing over open wounds, and allowing the

surrounding cambium to cover them up, as it will naturally do, the term of life of many a valuable tree can be prolonged, and its timber not only prevented from becoming diseased and deteriorating, but actually increased in value.

In the next chapter I propose to deal with the so-called "dry-rot" in timber which has been felled and cut up—a disease which has produced much distress at various times and in various countries.

CHAPTER VII.

THE "DRY-ROT" OF TIMBER.

It has long been known that timber which has been felled, sawn up, and stored in wood-yards, is by no means necessarily beyond danger, but that either in the stacks, or even after it has been employed in building construction, it may suffer degeneration of a rapid character from the disease known generally as "dry-rot." The object of the present chapter is to throw some light on the question of dry-rot, by summarizing the chief results of recent botanical inquiries into the nature and causes of the disease—or, rather, diseases, for it will be shown that there are several kinds of so-called "dry-rot."

The usual signs of the ordinary dry-rot of timber in buildings, especially deal-timber or fir-wood, are as follows. The wood becomes darker in colour, dull yellowish-brown instead of the paler tint of sound

deal; its specific weight diminishes greatly, and that this is due to a loss of substance can be easily proved directly. These changes are accompanied with a cracking and warping of the wood, due to the shortening of the elements as their water evaporates and they

FIG. 21.—Portion of the mycelium of *Merulius lacrymans* removed from the surface of a beam of wood. This cake-like mass spreads over the surface of the timber, to which it is intimately attached by hyphæ running in the wood-substance. Subsequently it develops the spore-bearing areolæ near its edges. The shading indicates differences in colour, as well as irregularities of surface.

part from one another: if the disease affects one side of a beam or plank, these changes cause a pronounced warping or bending of the timber, and in bad cases it

looks as if it had been burnt or scorched on the injured side. If the beam or plank is wet, the diseased parts are found to be so soft that they can easily be cut with a knife, almost like cheese; when dry, however, the touch of a hard instrument breaks the wood into brittle fibrous bits, easily crushed between the fingers to a yellow-brown, snuff-like powder. The timber has by this time lost its coherence, which, as we have seen, depends on the firm interlocking and holding together of the uninjured fibrous elements, and may give way under even light loads—a fact only too well known to builders and tenants. The walls of the wood-elements (tracheides, vessels, fibres, or cells, according to the kind of timber, and the part affected) are now, in fact, reduced more or less to powder, and if such badly diseased timber is placed in water it rapidly absorbs it and sinks: the wood in this condition also readily condenses and absorbs moisture from damp air, a fact which we shall see has an important bearing on the progress of the disease itself.

If such a piece of badly diseased deal as I have shortly described is carefully examined, the observer is easily convinced that fungus filaments (mycelium) are present in the timber, and the microscope shows that the finer filaments of the mycelium (hyphæ) are permeating the rotting timber in all directions—run-

ning between and in the wood elements, and also on the surface, and there forming cake-like masses (Fig. 21). In a vast number of cases, longer or shorter, broader or narrower, cords of greyish-white mycelium may be seen coursing on the surface and in the cracks: in course of time there will be observed flat cake-like masses of this mycelium, the hyphæ being woven into felt-like sheets, and these may be extending themselves on to neighbouring pieces of timber, or even on the brick-work or ground on which the timber is resting. These cord-like strands and cake-like masses of felt, with their innumerable fine filamentous continuations in the wood, constitute the vegetative body or mycelium of a fungus known as *Merulius lacrymans*. Under certain circumstances, often realized in cellars and houses, the cakes of mycelium are observed to develop the fructification of the fungus illustrated in Fig. 22.

To understand the structure of this fructification we may contrast it with that of the *Polyporus* or *Trametes* referred to in Chapters V. and VI.; where in the latter we find a number of pores leading each into a tubular cavity lined with the cells which produce the spores, the *Merulius* shows a number of shallow depressions lined by the spore-forming cells. The ridges which separate these depressed areolæ have a more or less zigzag course, running together, and sometimes the

whole presents a likeness to honey-comb; if the ridges were higher, and regularly walled in the

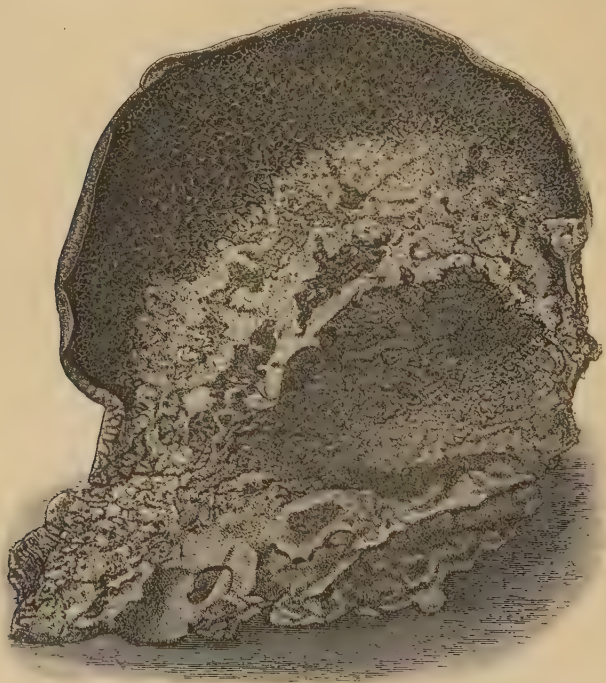

FIG. 22.—Mature fructification of *Merulius lacrymans*. The cake-like mass of felted mycelium has developed a series of areolæ (in the upper part of the figure) on the walls of which the spores are produced. In the natural position this spore-bearing layer is turned downwards, and in a moist environment pellucid drops or "tears" distil from it. The barren part in the foreground was on a wall, and the remainder on the lower side of a beam: the fungus was photographed in this position to show the areolation.

depressed areas, the structure would correspond to that of a *Polyporus* in essential points. The spores

are produced in enormous numbers (Fig. 23, A) on this areolated surface, which is directed downwards, and is usually golden-brown, but may be dull in colour, and presents the remarkable phenomenon of exuding drops of clear water, like tears, whence the name *lacrymans*. In well-grown specimens, such as may sometimes be observed on the roof of a cellar, these crystal-like tears hang from the areolated surface like pendants, and give an extraordinarily beautiful appearance to the whole ; the substance of the glistening *Merulius* may then be like shot-velvet gleaming with bright tints of yellow, orange, and even purple.

It has now been demonstrated by actual experiment that the spores of the fungus, *Merulius lacrymans*, will germinate on the surface of damp timber, and send their germinal filaments into the tracheides, boring through the cell-walls (Fig. 23, D), and extending rapidly in all directions. The fungus mycelium, as it gains in strength by feeding upon the substance of these cell-walls, destroys the wood by a process very similar to that already described (compare Fig. 14).

It appears, however, from the investigations of Poleck and Hartig, that certain conditions are absolutely necessary for the development of the mycelium and its spread in the timber, and there can be no question that the intelligent application of the

knowledge furnished by the scientific elucidation of the biology of the fungus is the key to successful treatment of the disease. This is, of course, true of all the diseases of timber, so far as they can be dealt

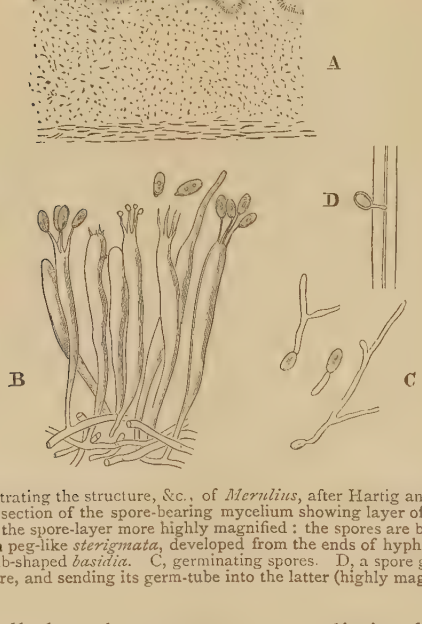

FIG. 23.—Illustrating the structure, &c., of *Merulius*, after Hartig and Poleck. A, transverse section of the spore-bearing mycelium showing layer of spores above. B, part of the spore-layer more highly magnified: the spores are borne in groups of four, on peg-like *sterigmata*, developed from the ends of hyphæ, which swell up into club-shaped *basidia*. C, germinating spores. D, a spore germinating on a wood-fibre, and sending its germ-tube into the latter (highly magnified).

with at all, but it comes out so distinctly in the present case that it will be well to examine a little at length some of the chief conclusions.

Merulius, like all fungi, consists of relatively large

quantities of water—50 to 60 per cent. of its weight at least—together with much smaller quantities of nitrogenous and fatty substances and cellulose, and minute but absolutely essential traces of mineral matters, the chief of which are potassium and phosphorus. It is not necessary to dwell at length on the exact quantities of these matters found by analysis, nor to mention a few other bodies of which traces exist in such fungi. The point just now is that all these materials are formed by the fungus at the expense of the substance of the wood, and for a long time there was considerable difficulty in understanding how this could come about.

The first difficulty was that although the "dry-rot fungus" could always be found, and the mycelium was easily transferred from a piece of diseased wood to a piece of healthy wood provided they were in a suitable warm, damp, still atmosphere, no one had as yet succeeded in causing the spores of the *Merulius* to germinate, or in following the earliest stages of the disease. Up to about the end of the year 1884 it was known that the spores refused to germinate either in water or in decoctions of fruit; and repeated trials were made, but in vain, to see them actually germinate on damp wood, until two observers, Poleck and Hartig, discovered about the same time the necessary conditions for germination. It should be noted here

that this difficulty in persuading spores to germinate is by no means an isolated instance: we are still ignorant of the conditions necessary for the germination of the spores of many fungi—*e.g.* the spores of the mushroom, according to De Bary; and it is known that in numerous cases spores need very peculiar treatment before they will germinate. The peculiarity in the case of the spores of *Merulius lacrymans* was found by Hartig to be the necessity of the presence of an alkali, such as ammonia; and it is found that in cellars, stables, and other outhouses where ammoniacal or alkaline emanations from the soil or elsewhere can reach the timber, there is a particularly favourable circumstance afforded for the germination of the spores. The other conditions are provided by a warm, still, damp atmosphere, such as exists in badly ventilated cellars, and corners, and beneath the flooring of many buildings.

Careful experiments have shown beyond all question that the "dry-rot fungus" is no exception to other fungi with respect to moisture: thoroughly dry timber, so long as it is kept thoroughly dry, is proof against the disease we are considering. Nay, more, the fungus is peculiarly susceptible to drought, and the mycelial threads and even the young fructifications growing on the surface of a beam of timber in a

damp close situation may be readily killed in a day or two by letting in thoroughly dry air: of course, the mycelium deeper down in the wood is not so easily and quickly destroyed, since not only is it more protected, but the mycelial strands are able to transport moisture from a distance. Much misunderstanding prevails as to the meaning of "dry air" and "dry wood": as a matter of fact the air usually contains much moisture, especially in cellars and quiet corners devoid of draughts, such as *Merulius* delights in, and we have already seen how dry timber rapidly absorbs moisture from such air. Moreover, the strands of mycelium may extend into damp soil, foundations, brick-work, &c.; in such cases they convey moisture to parts growing in apparently dry situations.

A large series of comparative experiments, made especially by Hartig, have fully established the correctness of the conclusion that damp foundations, walls, &c., encourage the spread of dry-rot, quite independently of the quality of the timber. This is important, because it has long been supposed that timber felled in summer was more prone to dry-rot than timber felled in winter: such, however, is not shown to be the case, for under the same conditions both summer- and winter-wood suffer alike, and

decrease in weight to the same extent during the progress of the disease. There is an excellent opportunity for further research here however, since one observer maintains that in one case at any rate (*Pinus sylvestris*) the timber felled at the end of April suffered from the disease, whereas that felled in winter resisted the attacks of the fungus: internal evidence in the published account supports the suspicion that some error occurred here. The wood which succumbed was found to contain much larger quantities of potassium and phosphorus (two important ingredients for the fungus), and Poleck suggests that this difference in chemical constitution explains the ease with which his April specimens were infected.

It appears probable from later researches and criticism that Poleck did not choose the same parts of the two stems selected for his experiments, for (in the case of *Pinus sylvestris*) the heart-wood is attacked much less energetically than the sap-wood—a circumstance which certainly may explain the questionable results if the chemist paid no attention to it, but analyzed the sap-wood of one and the heart-wood of the other piece of timber, as he seems to have done.

The best knowledge to hand seems to be that no difference is observable in the susceptibility to dry-rot

of winter-wood and summer-wood of the same timber; *i.e. Merulius lacrymans* will attack both equally, if other conditions are the same.

But air-dry and thoroughly seasoned timber is much less easily attacked than damp fresh cut wood of the same kind, both being exposed to the same conditions.

Moreover, different timbers are attacked and destroyed in different degrees. The heart-wood of the pine is more resistant than any spruce timber. Experimental observations are wanted on the comparative resistance of oak, beech, and other timbers, and indeed the whole of this part of the question is well worth further investigation.

When the spore has germinated, and the fungus hyphæ have begun to grow and branch in the moist timber, they proceed at once to destroy and feed upon the contents of the medullary rays; the cells composing these contain starch and saccharine matters, nitrogenous substances, and inorganic elements, such as potassium, phosphorus, calcium, &c. Unless there is any very new and young wood present, this is the only considerable source of proteid substances that the fungus has: no doubt a little may be obtained from the resin-passages, but only the younger ones. In accordance with this a curious fact

was discovered by Hartig : the older parts of the hyphæ pass their protoplasmic contents on to the younger growing portions, and so economize the nitrogenous substances. Other food-substances are not so sparse ; the lignified walls inclose water and air, and contain mineral salts, and such organic substances as coniferin, tannin, &c., and some of these are absorbed and employed by the fungus. Coniferin especially appears to be destroyed by the hyphæ.

The structure of the walls of the tracheides and cells of the wood is completely destroyed as the fungus hyphæ extract the minerals, cellulose, and other substances from them. The minerals are absorbed at points of contact between the hyphæ and the walls, reminding us of the action of roots on a marble plate: the coniferin and other organic substances are no doubt first rendered soluble by a ferment, and then absorbed by the hyphæ. This excretion of ferment has nothing to do with the excretion of water in the liquid state, which gives the fungus its specific name : the "tears" themselves have no solvent action on wood.

It will be evident from what has been stated that the practical application of botanical knowledge is here not only possible, but much easier than is the case in dealing with many other diseases.

It must first be borne in mind that this fungus spreads, like so many others, by means of both spores and mycelium: it is easy to see strands of mycelium passing from badly-diseased planks or beams, &c., across intervening brick-work or soil, and on to sound timber, which it then infects. The spores are developed in countless myriads from the fructifications described, and they are extremely minute and light: it has been proved that they can be carried from house to house on the clothes and tools, &c., of workmen, who in their ignorance of the facts are perfectly careless about laying their coats, implements, &c., on piles of the diseased timber intended for removal. Again, in replacing beams, &c., attacked with dry-rot, with sound timber, the utmost ignorance and carelessness are shown: broken pieces of the diseased timber are left about, whether with spores on or not; and I have myself seen quite lately sound planks laid close upon and nailed to planks attacked with the "rot." Hartig proved that the spores can be carried from the wood of one building to that of another by means of the saws of workmen.

But perhaps the most reckless of all practices is the usage of partially diseased timber for other constructive purposes, and stacking it meanwhile in a yard or outbuilding in the neighbourhood of fresh-cut,

unseasoned timber. It is obvious that the diseased timber should be removed as quickly as possible, and burnt at once: if used as firewood in the ordinary way, it is at the risk of those concerned. Of course the great danger consists in the presence of many ripe spores, and their being scattered on timber which is under proper conditions for their germination and the spread of the mycelium.

It is clearly an act worthy only of a madman to use fresh "green" timber for building purposes; but it seems certain that much improperly dried and by no means "seasoned" timber is employed in some modern houses. Such wood is peculiarly exposed to the attacks of any spores or mycelium that may be near.

But even when the beams, door-posts, window-sashes, &c., in a house are made of properly dried and seasoned deal, the danger is not averted if they are supported on damp walls or floors. For the sake of illustration I will take an extreme case, though I have no doubt it has been realized at various times. Beams of thoroughly seasoned deal are cut with a saw which has previously been used for cutting up diseased timber, and a few spores of *Merulius* are rubbed off from the saw, and left sticking to one end of the cut beam: this end is then laid on or in a

brick wall, or foundation, which has only stood long enough to partially dry. If there is no current of dry air established through this part, nothing is more probable than that the spores will germinate, and the mycelium spread, and in the course of time—it may be months afterwards—a mysterious outbreak of dry-rot ensues. There can be no question that the ends of beams in new houses are peculiarly exposed to the attacks of dry-rot in this way.

The great safeguard—beyond taking care that no spores or mycelium are present from the first—is to arrange that all the brick-work, floors, &c., be thoroughly dry before the timber is put in contact with them; or to interpose some impervious substance—a less trustworthy method. Then it is necessary to aërate and ventilate the timber; for *dry* timber *kept dry* is proof against "dry-rot."

The ventilation must be real and thorough however, for it has been by no means an uncommon experience to find window-sashes, door-posts, &c., in damp buildings, with the insides scooped out by dry-rot, and the aërated outer shells of the timber quite sound: this is undoubtedly often due to the paint on the outer surfaces preventing a thorough drying of the deeper parts of the wood.

Of course the question arises, and is loudly urged,

Is there no medium which will act as an antiseptic, and kill the mycelium in the timber in the earlier stages of the disease? The answer is, that mineral poisons will at once kill the mycelium on contact, and that creosote, &c., will do the same; but who will take the trouble to thoroughly impregnate timber in buildings such as harbour dry-rot? And it is simply useless to merely paint these specifics on the surface of the timber: they soak in a little way, and kill the mycelium on the outside, but that is all, and the deadly rot goes on destroying the inner parts of the timber just as surely.

There is one practical suggestion in this connection, however; in cases where properly seasoned timber is used, the beams laid in the brick walls might have their ends creosoted, and if thoroughly done this would probably be efficacious during the dangerous period while the walls finished drying. I believe this idea has been carried out lately by Prof. Hartig, who told me of it. The same observer was also kind enough to show me some of his experiments with dry-rot and antiseptics: he dug up and examined in my presence glass jars containing each two pieces of deal—one piece sound, and the other diseased. The sound pieces had been treated with various antiseptics, and then tied face to face with the diseased

pieces, and buried in the jar for many months or even two years.

However, I must now leave this part of the subject, referring the reader to special publications for further information, and pass on to a sketch of what is known of other kinds of "dry-rot." It is a remarkable fact, and well known, that *Merulius lacrymans* is a domestic fungus, peculiar to dwelling-houses and other buildings, and not found in the forest. We may avoid the discussion as to whether or no it has ever been found wild : one case, it is true, is on record on good authority, but the striking peculiarity about it is that, like some other organisms, this fungus has become intimately associated with mankind and human dwellings, &c.

The case is very different with the next disease-producing fungus I propose to consider. It frequently happens that timber which has been stacked for some time in the wood-yards shows red or brown streaks, where the substance of the timber is softer, and in fact may be "rotten": after passing through the saw-mill these streaks of bad wood seriously impair the value of the planks, beams, &c., cut from the logs.

Prof. Hartig, who has devoted much time to the investigation of the various forms of "dry-rot," has shown that this particular kind of red or brown streaking is due to the ravages of *Polyporus vaporarius*. The

mycelium of this fungus destroys the structure of the wood in a manner so similar to that of the *Merulius* that the sawyers and others do not readily distinguish

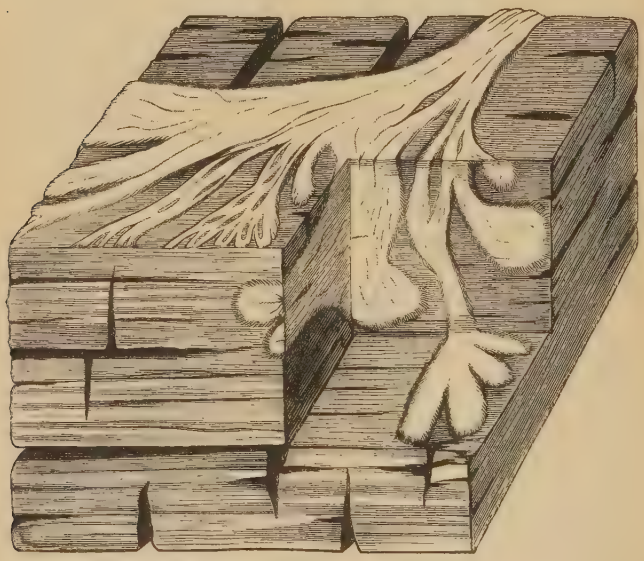

FIG. 24.—A piece of pine-wood attacked by the mycelium of *Polyporus vaporarius*. The timber has warped and cracked under the action of the fungus, becoming of a warm brown colour at the same time; in the crevices the white strands of felt-like mycelium have then increased, and on splitting the diseased timber they are found creeping and applying themselves to all the surfaces. Except that the colour is snowy white, instead of gray, this mycelium may easily be mistaken for that of *Merulius*. The fructification which it develops is, however, very different. (After R. Hartig)

between the two. The mycelium of *Polyporus vaporarius* forms thick ribbons and strands, but they are snowy white, and not gray like those of

Merulius lacrymans: the structure, &c., of the fructification are also different. I have shown in Fig. 24 a piece of wood undergoing destruction from the action of the mycelium of this *Polyporus*, and it will be seen how the diseased timber cracks just as under the influence of *Merulius*.

Now *Polyporus vaporarius* is common in the forests, and it has been found that its spores may lodge in cracks in the barked logs of timber lying on the ground—cracks such as those in Fig. 1, p. 3). In the particular forests of which the following story is told, the felling is accomplished in May (because the trunks can then be readily barked, and also because such work cannot be carried on there in the winter), and the logs remain exposed to the sun and rain, and vicissitudes of weather generally, for some time. Now it is easy to see that rain may easily wash spores into such cracks as those referred to, and the fungus obtains its hold of the timber in this way.

The next stage is sending the timber down to the timber-yards, and this is accomplished, in the districts referred to, by floating the logs down the river. Once in the river, the wood swells, and the cracks close up; but the fungus spores are already deeply imprisoned in the cracks, and have no doubt by this time

emitted their germinal hyphæ, and commenced to form the mycelium. This may or may not be the case : the important point is simply that the fungus is already there. Having arrived at the timber-wharves the logs are stacked for sawing in heaps as big as houses : after a time the sawing up begins. It usually happens that the uppermost logs when cut up show little or no signs of rot ; lower down, however, red and brown streaks appear in the planks, and when the lowermost logs are reached, perhaps after some weeks or months, deep channels of powdery, rotten wood are found, running up inside the logs in such a way that their transverse sections often form triangular or V-shaped figures, with the apex of the triangle or V turned towards the periphery of the log.

The explanation is simple. The uppermost logs on the stack have dried sufficiently to arrest the progress of the mycelium, and therefore of the disease : the lower logs, however, kept damp and warm by those above, have offered every chance to the formation and spread of the mycelium deep down in the cracks of the timber. I was much impressed with this ingenious explanation, first given to me by Prof. Hartig, and illustrated by actual specimens. It will be noticed how fully it explains the curious shape of the rotten courses because the

depths of the cracks are first diseased, and the mycelium spreads thence.

Obviously some protection would be afforded if the bark could be retained on the felled logs, or if they could be at once covered and kept covered after bark-

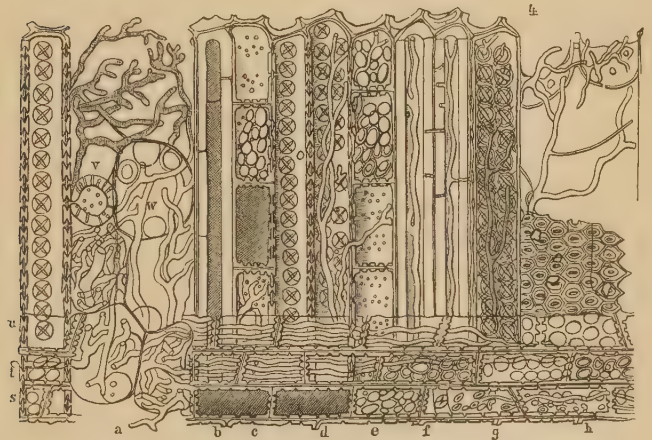

FIG. 25.—Part of a longitudinal radial section through a piece of wood infected with *Polyporus igniarius*. After Hartig (highly magnified).

ing ; and, again, something towards protection might be done by carting instead of floating the timber, when possible. At the same time, this is not a reliable mode of avoiding the disease by itself ; and even the dry top logs in the saw-yard are not safe. Suppose the following case. The top logs of the stack are

quite dry, and are cut into beams and used in building; but they have spores or young mycelium trapped in the cracks at various places. If, from contact with damp brick-work or other sources of moisture, these dormant spores or mycelia are enabled to spread subsequently, we may have "dry-rot" in the building; but this "dry-rot" is due to *Polyporus vaporarius*, and not to the well-known *Merulius lacrymans*.

There can probably be no question of the advantage of creosoting the ends of such rafters, beams, &c.; since the creosote will act long enough to enable the timber to dry, if it is ever to dry at all. But the mycelium of *Polyporus vaporarius* makes its way into the still standing timber of pines and firs; for it is a wound-parasite, and its mycelium can obtain a hold at places which have been injured by the bites of animals, &c.: it thus happens that this form of "dry-rot" is an extremely dangerous and insidious one, and I have little doubt that it costs our English timber-merchants something, as well as Continental ones. Nor are the above the only kinds of "dry-rot" we know. A disease of pine-wood is caused by *Polyporus mollis*, which is very similar to the last in many respects, and the suspicion may well gain ground that this important subject has by no means been exhausted yet.

CHAPTER VIII.

THE CORTEX AND BARK OF TREES.

If we turn our attention for a moment to the illustrations in the first chapter, it will be remembered that our typical log of timber was clothed in a sort of jacket termed the cortex, the outer parts of which constitute what is generally known as the bark. This cortical covering is separated from the wood proper by the cambium, and I pointed out (pp. 11 and 12) that the cells produced by divisions on the outside of the cambium cylinder are employed to add to the cortex.

Now this cortical jacket is a very complicated structure, since it not only consists of numerous elements, differing in different trees, but it also undergoes some very curious changes as the plant grows up into a tree. It is beyond the purpose of this book to enter in detail into these anatomical matters, however; and I must refer the reader to special text-books for

them, simply contenting myself here with general truths which will serve to render clearer certain statements which are to follow.

It is possible to make two generalizations, which apply not only to the illustration (Fig 26) here selected but also to most of our timber-trees. In the first place, the cortical jacket, taken as a whole, consists not of rigid lignified elements such as the tracheides and fibres of the wood, but of thin-walled, soft, elastic elements of various kinds, which are easily compressed or displaced, and for the most part easily killed or injured—I say for the most part easily injured, because, as we shall see immediately, a reservation must be made in favour of the outermost tissues, or cork and bark proper, which are by no means so easily destroyed, and act as a protection to the rest.

The second generalization is, that since the cambium adds new elements to the cortex on the inside of the latter, and since the cambium cylinder as a whole is travelling radially outwards—*i.e.* further from the pith—each year, as follows from its mode of adding the new annual rings of rigid wood on to the exterior of the older ones, it is clear that the cortical jacket as a whole must suffer distension from within, and tend to become too small for the enlarging cylinder of rigid wood and growing cambium combined. Indeed,

it is not difficult to see that, unless certain provisions are made for keeping up the continuity of the cortical tissues, they must give way under the pressure from within. As we shall see, such a catastrophe is in part prevented by a very peculiar and efficient process.

Before we can understand this, however, we must take a glance at the structural characters of the whole of this jacket (Fig. 26). While the branch or stem is still young, it may be conveniently considered as consisting of three chief parts.

(1) On the outside is a thin layer of flat, tabular cork-cells (Fig. 26, *Co*), which increase in number by the activity of certain layers of cells along a plane parallel to the surface of the stem or branch. These cells(*C.Ca*) behave very much like the proper cambium, but the cells divided off from them do not undergo the profound changes suffered by those which are to become elements of the wood and inner cortex. The cells formed on the outside of the line *C.Ca* in fact simply become cork-cells ; while those formed on the inside of the line *C.Ca* become living cells (*Cl*) very like those I am now going to describe.

(2) Inside this cork-forming layer is a mass of soft, thin-walled, "juicy" cells, *pa*, which are all living, and most of which contain granules of chlorophyll, and thus give the green colour to the young cortex—a

colour which becomes toned down to various shades of olive, gray, brown, &c., as the layers of cork increase with the age of the part. It is because the corky layers are becoming thicker that the twig passes from green to gray or brown as it grows older. Now these green living cells of the cortex are very important for our purpose, because, since they contain much food-material and soft juicy contents of just the kind to nourish a parasitic fungus, we shall find that, whenever they are exposed by injury, &c., they constitute an important place of weakness—nay, more, various fungi are adapted in most peculiar ways to get at them. Since these cells are for the most part living, and capable of dividing, also, we have to consider the part they play in increasing the extent of the cortex.

(3) The third of the partly natural, partly arbitrary portions into which we are dividing the cortical jacket is found between the green, succulent cells (*pa*) of the cortex proper (which we have just been considering), and the proper cambium, *Ca*, and it may be regarded as entirely formed directly from the cambium-cells. These latter, developed in smaller numbers on the outside, towards the cortex, than on the inside, towards the wood, undergo somewhat similar changes in shape to those which go to add to the wood, but they show the important differences that their walls remain un-

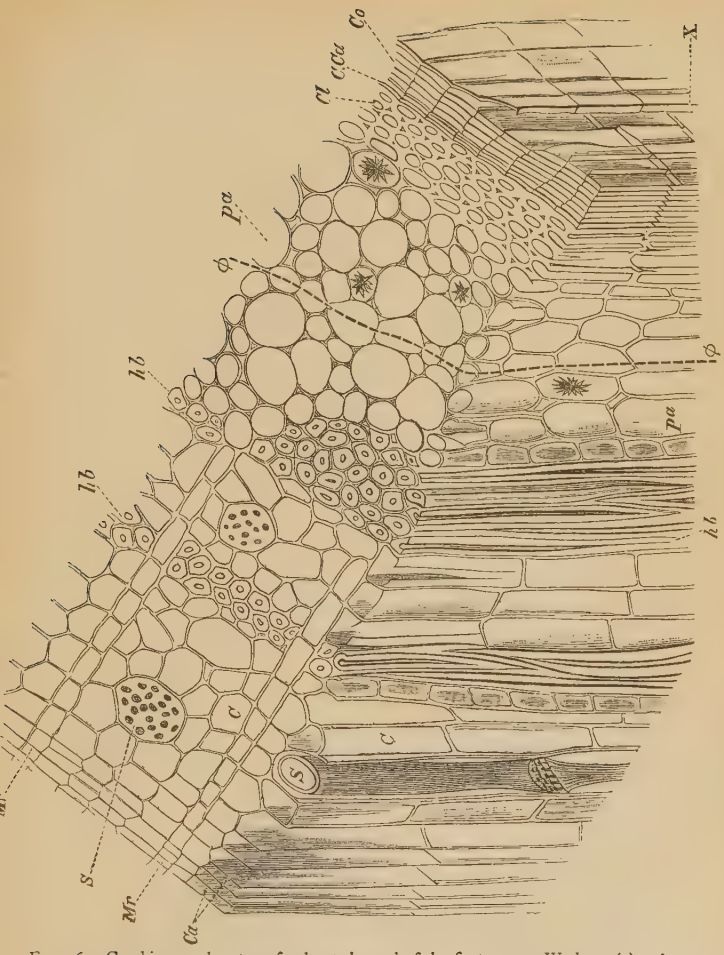

FIG. 26.—Cambium and cortex of oak, at the end of the first year. We have (1) cork-cells (*X*), formed from the cork-cambium (*C.Ca*): the cells developed on the inside of the latter (*Cl*) are termed collenchyma, and add to the cortex. (2) The cortex proper, consisting of parenchyma-cells (*pa*), some of which contain crystals. (3) The inner or secondary cortex (termed *phloem* or bast), developed chiefly by the activity of the cambium (*Ca*): this phloem consists of hard bast fibres (*hb*), sieve-tubes (*S*), and cells (*c*), and is added to internally by the cambium (*Ca*) each year. It is also traversed by medullary-rays (*Mr*), which are continuations of those in the wood. The dotted line (ϕ) in the cortical parenchyma indicates where the new cork-cambium will be developed.

lignified, and for the most part very thin and yielding, and retain their living contents. For the rest, we may neglect details and refer to the illustration for further particulars. The tissue in question is marked by *S*, *c*, *hb* in the figure, and is called *phloem* or bast.

A word or two as to the functions of the cortex, though the subject properly demands much longer discussion. It may be looked upon as especially the part through which the valuable substances formed in the leaves are passing in various directions to be used where they are wanted. When we reflect that these substances are the foods from which everything in the tree—new cambium, new roots, buds, flowers, and fruit &c.—are to be constructed, it becomes clear that if any enemy settles in the cortex and robs it of these substances, it reduces not only the general powers of the tree, but also—and this is the point which especially interests us now—its timber-producing capacity. In the same way, anything which cuts or injures the continuity of the cortical layers results in diverting the nutritive substances into other channels. A very large class of phenomena can be explained if these points are understood, which would be mysterious, or at least obscure, otherwise.

Having now sketched the condition of this cortical jacket when the branch or stem is still young, it will

be easy to understand broadly what occurs as it thickens with age.

In the first place, it is clear that the continuous sheet of cork (*Co*) must first be distended, and finally ruptured, by the increasing pressure exerted from within: it is true, this layer is very elastic and extensible, and impervious to water or nearly so—in fact it is a thin layer or skin, with properties like those of a bottle cork—but even it must give way as the cylinder goes on expanding, and it cracks and peels off. This would expose the delicate tissues below, if it were not for the fact that another layer of cork has by this time begun to form below the one which is ruptured: a cork-forming layer arises along the line ϕ, and busily produces another sheet of this protective tissue in a plane more or less parallel with the one which is becoming cracked. This new cork-forming tissue behaves as before: the outer cells become cork, the inner ones add to the green succulent parenchyma-cells (*pa*). As years go on, and this layer in its turn splits and peels, others are formed further inwards; and if it is remembered that a layer of cork is particularly impervious to water and air, it is easy to understand that each successive sheet of cork cuts off all the tissues on its exterior from participation in the life processes of the plant, and they therefore die:

consequently we have a gradually increasing *bark* proper, formed of the accumulated cork-layers and other dead tissues.

A great number of interesting points, important in their proper connections, must be passed over here. Some of these refer to the anatomy of the various "barks"—the word "bark" being commonly used in commerce to mean the whole of the cortical jacket—the places of origin of the cork-layer, and the way in which the true bark peels off: those further interested here may compare the plane, the birch, the Scotch pine, and the elm, for instance, with the oak. Other facts have reference to the chemical and other substances found in the cells of the cortex, and which make "barks" of value commercially. I need only quote the alkaloids in Cinchona, the fibres in the Malvaceæ, the tannin in the oaks, the colouring-matter in *Garcinia* (gamboge), the gutta-percha from *Isonandra*, the ethereal oil of cinnamon, as a few examples in this connection, since our immediate subject does not admit of a detailed treatment of these extremely interesting matters.

The above brief account may suffice to give a general idea of what the cortical jacket covering our timber is, and how it comes about that in the normal case the thickening of the cylinder is rendered possible without

exposing the cambium and other delicate tissues: it may also serve to show why bark is so various in composition and other characters. But it is also clear that this jacket of coherent bark, bound together by the elastic sheets of cork, must in its turn exert considerable pressure as it reacts on the softer, living, succulent parts of the cortex, trapped as they are between the rigid wood cylinder and the bark proper; and it is easy to convince ourselves that such is the case. By simply cutting a longitudinal slit through the cortex, down to near the cambium, but taking care not to injure the latter, the following results may be obtained. First, the bark gapes, the raw edges of the wound separating and exposing the tissues below; next, in course of time the raw edges are seen to be healed over with cork—produced by the conversion of the outer living cells of the cortex into cork-cells. As time passes, provided no external interference occurs, the now rounded and somewhat swollen cork-covered edges of the wound will be found closing up again; and sooner or later, depending chiefly on the extent of the wound and the vigour of the tree, the growing lips of the wound will come together and unite completely.

But examination will show that although such a slit-wound is so easily healed over, it has had an effect on

the wood. Supposing it has required three years to heal over, it will be found that the new annual rings of wood are a little thicker just below the slit; this is simply because the slit had relieved the pressure on the cambium. The converse has also been proved to be true—*i.e.* by increasing the pressure on the cambium by means of iron bands, the annual rings below the bands are thinner and denser than elsewhere.

But we have also seen that the cambium is not the only living tissue below the bark: the cortical parenchyma (*pa*), and the cells (*c*) of the inner cortex (technically the phloem) are all living and capable of growth and division, as was described above. The release from pressure affects them also; in fact, the "callus," or cushion of tissue which starts from the lips of the wound and closes it over, simply consists of the rapidly growing and dividing cells of this cortex, *i.e.* the release from pressure enables them to more than catch up the enlarging layer of cortex around the wound.

An elegant and simple instance of this accelerated growth of the cortex and cambium when released from the pressure of other tissues is exhibited in the healing over of the cut ends of a branch, a subject to be dealt with in the next chapter; and the whole practice of propagation by slips or cuttings, the renewal of the

"bark" of Cinchonas, and other economic processes, depend on these matters.

In anticipation of some points to be explained only if these phenomena are understood, I may simply remark here that, obviously, if some parasite attacks the growing lips of the "callus" as it is trying to cover up the wound, or if the cambium is injured below, the pathological disturbances thus introduced will modify the result: the importance of this will appear when we come to examine certain disturbances which depend upon the attacks of Fungi which settle on these wounds before they are properly healed over. In concluding this brief sketch of a large subject, it may be noted that, generally speaking, what has been stated of branches, &c., is also true of roots; and it is easy to see how the nibbling or gnawing of small animals, the pecking of birds, abrasions, and numerous other things, are so many causes of such wounds in the forest.

CHAPTER IX.

THE HEALING OF WOUNDS BY OCCLUSION.

If we pass through a forest of oaks, beeches, pines, and other trees, it requires but a glance here and there to see that various natural processes are at work to reduce the number of branches as the trees become older. Every tree bears more buds than develop into twigs and branches, for not only do some of the buds at a very early date divert the food-supplies from others, and thus starve them off, but they are also exposed to the attacks of insects, squirrels, &c., and to dangers arising from inclement weather, and from being struck by falling trees and branches, &c., and many are thus destroyed. Such causes alone will account in part for the irregularity of a tree, especially a Conifer, in which the buds may have been developed so regularly that if all came to maturity the tree would be symmetrical. But that this is not the whole of the case, can be

easily seen, and is of course well known to every gardener and forester.

If we remove a small branch of several years' growth from an oak, for instance, it will be noticed that on the twigs last formed there is a bud at the axil of every leaf; but on examining the parts developed two or three years previously it is easy to convince ourselves of the existence of certain small scars, above the nearly obliterated leaf-scars, and to see that if a small twig projected from each of these scars the symmetry of the branching might be completed. Now it is certain that buds or twigs were formed at these places, and we know from careful observations that they have been naturally thrown off by a process analogous to the shedding of the leaves; in other words the oak sheds some of its young branches naturally every year. And many other trees do the same; for instance, the black poplar, the Scotch pine, *Dammara*, &c.; in some trees, indeed, and notably in the so-called swamp cypress (*Taxodium distichum*) of North America, the habit is so pronounced that it sheds most of its young branches every year.

But apart from these less obvious causes for the suppression of branches, we notice in the forest that the majority of the trees have lost their lower branches at a much later date, and that in many cases the

remains of the proximal parts of the dead branches are sticking out from the trunk like unsightly wooden horns. Some of these branches may have been broken off by the fall of neighbouring trees or large limbs; others may have been broken by the weight of snow

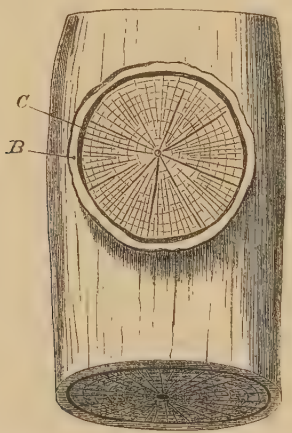

FIG. 27.—Portion of a tree from which a branch has been cut off close to the stem. *C*, the cambium of the branch; *B*, its cortex.

accumulating during the winter; others again, may have been broken by hand, or by heavy wind; and yet others have died off, in the first place because the overbearing shade of the surrounding trees cut off the access of light to their leaves, and secondly because the flow of nutritive materials to them ceased, being diverted into more profitable channels by the flourish-

ing, growing parts of the crown of leaves exposed to sunlight and air above.

The point I wish to insist upon here is that in these cases of branch-breaking, however brought about, open wounds are left exposed to all the vicissitudes of the forest atmosphere; if we compare the remnant of such a broken branch and the scar left after the natural shedding of a branch or leaf, the latter will be found covered with an impervious layer of cork, a tissue which keeps out damp, fungus-spores, &c., effectually.

It is, in fact—as a matter of observation and experiment—these open wounds which expose the standing timber to so many dangers from the attacks of parasitic fungi; and it will be instructive to look a little more closely into the matter as bearing on the question of the removal of large branches from trees.

If a fairly large branch of a tree, such as the oak, is cut off close to the trunk, a surface of wood is exposed, surrounded by a thin ring of cambium and bark (as in Figs. 27 and 28). We have already seen what the functions of the cambium are, and it will be observed that the cut edge of the cambium (*C*) is suddenly placed under different conditions from the usual ones; the chief change, and the only one we need notice at present, is that the cambium in the neighbourhood of

the cut surface is relieved from the compressing influence of the cortex and bark, and owing to this release of pressure it begins to grow out at the edges into a cushion or "callus," as shown in Figs. 29 and 30. A very similar "callus" is formed in the operation of

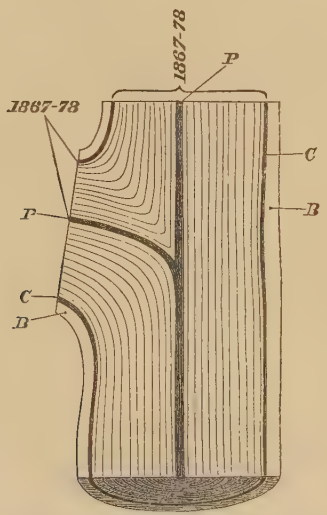

FIG. 28.—The same in longitudinal section. *P*, the pith of stem and branch; on either side of this are the twelve annual zones of wood produced during the years 1867–78, as marked. The cambium, *C*, separates these from the cortex, *B*.

multiplying plants by "cuttings," so well known to all: the cambium at the cut surface of the "slip" or "cutting" is relieved from the pressure of the cortex, and begins to grow out more rapidly in the directions of less pressure, and forms the callus.

Now this callus (Fig. 29, *Cal*) is in all cases something more than mere cambium—or rather, as the cambium extends by cell-divisions from the cut edge of the wound, its outer parts develop into cortex, and

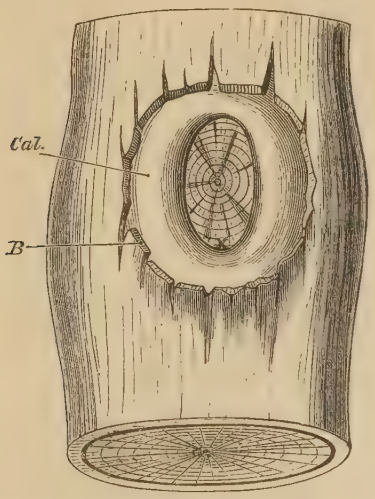

FIG. 29.—The same piece of stem four years later. The cushion-like development, *Cal*, resulting from the overgrowth of the cambium and cortical tissues of the cut branch, has extended some distance from the edges, and is covering in the exposed wood. *B* is the dead outer corky tissue, incapable of growth, and partially cracked under the pressures exerted by the thickening of the stem. The latter is somewhat swollen transversely, owing to the release of pressure in this region, enabling the cambium to develop a little more actively here; the quicker growth of the occluding cushion in the horizontal direction is due to the same cause.

its inner parts into wood, as in the normal case. The consequence is that we have in the callus, slowly creeping out from the margins of the wound, new

layers of wood and cortex with cambium between them (Fig. 30); and it will be noticed that each year the layer of wood extends a little further over the sur-

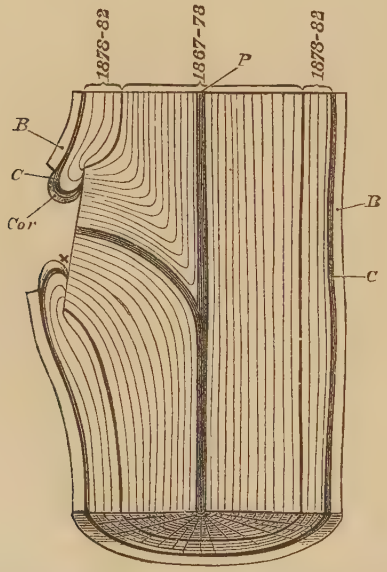

FIG. 30.—The same in longitudinal section; *P*, *B*, and *C* as before. The four new layers of wood formed during 1879–82 are artificially separated from the preceding by a stronger line. On the left side of the figure it will be noticed that the cambium (and therefore the wood developed from it) projected a little further over the cut end of the branch each year, carrying the cortical layers (*Cor*) with it. At +, in both figures, there is necessarily a depression in which rain-water, &c., is apt to lodge, and this is a particularly dangerous place, since fungus-spores may here settle and develop.

face of the wood of the wound, and towards the centre of the cut branch; and in course of time,

provided the wound is not too large, and the tree is full of vigour, the margins of the callus will meet near the middle, and what was the exposed cut surface of the branch will be buried beneath layers of new

FIG. 31.—The same piece of stem six years later still; the surface of the cut branch has now been covered in for some time, and only a boss-like projection marks where the previous cut surface was. This projection is protected by cork layers, like ordinary outer cortex, the old outer cortex cracking more and more as the stem expands.

wood and cortex, between which lies the cambium now once more continuous over the whole trunk of the tree (Figs. 31 and 32).

It is not here to the purpose to enter into the very

interesting histological questions connected with this callus-formation, or with the mechanical relations of

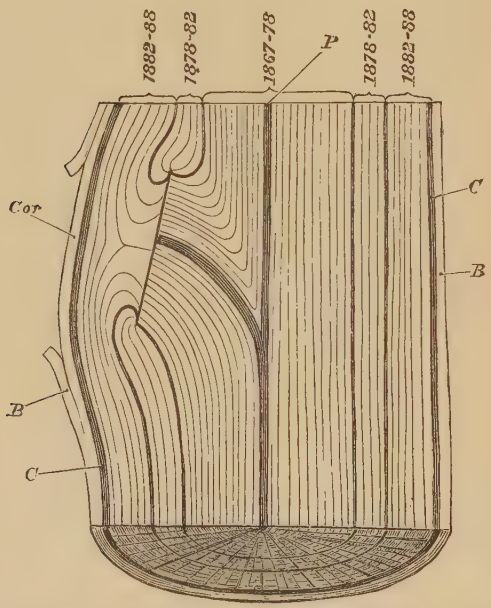

FIG. 32.—The same in longitudinal section: lettering as before. Six new layers of wood have been developed, and the cut end of the branch was completely occluded before the last three were formed—*i.e.* at the end of 1885. After that the cambium became once more continuous round the whole stem, and, beyond a slight protuberance over the occluded wound and the ragged edges of the dead corky outer layers, *B*, there are no signs of a breach.

the various parts one to another. It is sufficient for our present object to point out that this process of covering up, or *occlusion*, as I propose to term it,

requires some time for its completion. For the sake of illustration, I have numbered the various phases in the diagram, with the years during which the annual rings have been successively formed ; and it will be seen at a glance that in the case selected, it required seven years to cover up the surface of the cut branch (cf. Figs. 27–32). During these seven years more or less of the cut surface was exposed (Fig. 30) for some time to all the exigencies of the forest, and it will easily be understood that abundant opportunities were afforded during this interval for the spores of fungi to fall on the naked wood, and for moisture to condense and penetrate into the interior ; moreover, in the ledge formed at + in Figs. 29 and 30, by the lower part of the callus, as it slowly creeps up, there will always be water in wet weather ; and a sodden condition of the wood at this part is thus insured. All this is, of course, peculiarly adapted for the germination of spores ; and since the water will soak out nutritive materials, nothing could be more favourable for the growth and development of the mycelium of a fungus. These circumstances, favourable as they are for the fungi, are usually rendered even more so in practice, because the sawyers often allow such a branch to fall, and tear and crush the cambium and cortex at the lower edge of the wound. These and

other details must be passed over, however, and our attention be confined to the fact that there are ample chances for the spores of parasitic and other fungi to fall on a surface admirably suited for their development. The further fact must be insisted upon that numerous fungus-spores do fall and develop upon these wounds, and that by the time the exposed surface is covered in (as in Fig. 31) the timber is frequently already rotten, usually for some distance down into its substance. In the event of fungi, such as have been described above—parasites and wound-parasites—gaining a hold on such wounds, the ravages of the mycelium will continue after the occlusion is complete, and I have seen scores of trees apparently sound and whole when viewed from the exterior, the interior of which is a mere mass of rottenness: when a heavy gale at length blows them down, such trees are found to be mere hollow shells, the ravages of the mycelium having extended from the point of entry into every part of the older timber.

In a state of nature the processes above referred to do not go on so smoothly and easily as just described, and it will be profitable to glance at such a case as the following.

A fairly strong branch dies off, from any cause whatever—*e.g.* from being overshadowed by other

trees. All its tissues dry up, and its cortex, cambium, &c., are rapidly destroyed by saprophytic fungi, and in a short time we find only a hard, dry, branched stick projecting from the tree. At the extreme base,

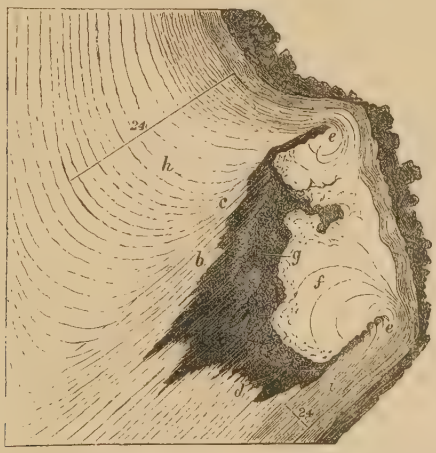

FIG. 33.—Base of a strong branch which had perished naturally twenty-four years previously to the stage figured. The branch decayed, and the base was gradually occluded by the thickening layers of the stem: the fall of the rotting branch did not occur till six years ago, however, and can be determined from the layers at *e* and *f*, which then began to turn inwards over the stump. Meanwhile, the base had become hollow and full of rotten wood, *g*. It is interesting to note how slight the growth is on the lower side of the branch base, *i*, as compared with that at *h* above: the line numbered 24 refers to the annual zones in each case. As seen at *b* and *d*, the rotting of the wood passes backwards, and may invade the previously healthy wood for some distance. (After Hartig.)

where it joins the tree, the tissues do not at once perish, but for a length of from half an inch to an inch or so the base is still nourished by the trunk. After a time, the wind, or a falling branch, or the

weight of accumulated snow, &c., breaks off the dead branch, leaving the projecting basal portion: if the branch broke off quite close to the stem, the wound would, or at least might, soon be occluded; but, as it is, the projecting piece not only takes longer to close in, but it tends to rot very badly (Fig. 33), and at the best forms a bad "knot" or hole in the timber when sawn up. Of course what has already been stated of cut branches applies here: the wounds are always sources of danger so long as they are exposed.

It is beyond the scope of this chapter to set forth the *pros* and *cons* as to the advisability of adopting any proposed treatment on a large scale: the simple question of cost will always have to be decided by those concerned. But whether it is practicable or not on a large scale, there is no question as to the desirability of adopting such treatment as the following to preserve valuable trees and timber from the ravages of these wound-parasites. Branches which break off should be cut close down to the stem, if possible in winter, and the clean cut made so that no tearing or crushing of the cambium and cortex occur; the surface should then be painted with a thorough coating of tar, and the wound left to be occluded. If the cutting is accomplished in spring or summer, trouble will be caused by the tar not sticking to the

damp surface. Although this is not an absolute safeguard against the attacks of fungi—simply because the germinal tubes from spores can find their way through small cracks at the margin of the wound, &c. —still it reduces the danger to a minimum, and it is certain that valuable old trees have been preserved in this way.

Before passing to treat of the chief diseases known to start from such wounds as the above, it should be remarked that it is not inevitable that the exposed surface becomes attacked by fungi capable of entering the timber. It happens not unfrequently that a good closure is effected over the cut base of a small branch in a few years, and that the timber of the base is sound everywhere but at the surface: this happy result may sometimes be attained in pines and other Conifers, for instance, by the exudation of resin or its infiltration into the wood; but in rarer cases it occurs even in non-resinous trees, and recent investigations go to show that the wood formed in these healing processes possesses the properties of true heart-wood. At the same time there is always danger, as stated, and we will now proceed to give a brief account of the chief classes of diseases to which such wounds render the tree liable.

The first and most common action is the decay

which sets in on the exposure of the wood surface to the alternate wetting and drying in contact with the atmosphere: it is known that wood oxidizes under such circumstances, and we may be sure that wounds are no exception to this rule. The surface of the wood gradually turns brown, and the structure of the timber is destroyed as the process extends.

The difficulty always arises in Nature, however, that mould-fungi and bacteria of various kinds soon co-operate with and hurry these processes, and it is impossible to say how much of the decay is due to merely physical and chemical actions, and how much to the fermentative action of these organisms. We ought not to shut our eyes to this rich field for investigation, although for the present purpose it suffices to recognize that the combined action of the wet, the oxygen of the air, and the fermenting action of the moulds and bacteria, &c., soon converts the outer parts of the wood into a mixture of acid substances resembling the humus of black leaf-mould.

Now as the rain soaks into this, it dissolves and carries down into the wood below certain bodies which are poisonous in their action on the living parts of the timber, and a great deal of damage may be caused by this means alone. But this is not all: as soon as the decaying surface of the wound provides these mixtures

of decomposed organic matter, it becomes a suitable soil for the development of fungi which are not parasitic—*i.e.* which cannot live on and in the normal and living parts of the tree—but which can and do thrive on partially decomposed wood. The spores of such fungi are particularly abundant, and many of the holes found in trees are due to their action. The hyphæ follow up the poisonous action of the juices referred to above, living on the dead tissues; and it will be intelligible that the drainage from the products aids the poisonous action as it soaks into the trunk. It is quite a common event to see a short stump, projecting from the trunk of a beech, for instance, the edges of the stump neatly rounded over by the action of a callus which was unable to close up in the middle, and to find that the hollow extends from the stump into the heart of the trunk for several feet or even yards. The hollow is lined by the decayed humus-like remains of the timber, caused by the action of such saprophytes as I have referred to. Similar phenomena occur in wounded or broken roots, and need not be described at length after what has been stated.

But, in addition to such decay as this, it is found that if the spores of true wound-parasites alight on the damp surface of the cut or broken branch, their

mycelium can extend comparatively rapidly into the still healthy and living tissues, bringing about the destructive influences described in previous chapters, and then it matters not whether the wound closes over quickly or slowly—the tree is doomed.

CHAPTER X.

"CANKER": THE LARCH DISEASE.

THERE is a large and important class of diseases of standing timber which start from the cortex and cambium so obviously that foresters and horticulturists, struck with the external symptoms, almost invariably term them "diseases of the bark"; and since most of them lead to the production of malformations and excrescences, often with outflowing of resinous and other fluids, a sort of rough superficial analogy to certain animal diseases has been supposed, and such terms as "canker," "cancer," and so forth, have been applied to them.

Confining our attention to the most common and typical cases, the following general statements may be made about these diseases. They usually result from imperfect healing of small wounds, the exposed cortex and cambium being attacked by some parasitic or

semi-parasitic fungus, as it tries to heal over the wound. The local disturbances in growth kept up by the mycelium feeding on the contents of the cells of these

FIG. 34.—Piece of tree stem affected with "canker." The injury commenced after the two inner zones of wood (1 and 2) had been developed: it extended further in successive periods of growth, as shown by the receding zones 3, 4, 5, and 6, until all the cambium and cortex was destroyed except the pieces *D* to *D*. *Cam*, cambium; *Cor*, living cortex; *D D*, dead tissues. At each period of growth the attempt has been made to heal over the wound, as shown by the successively receding lips.

tissues lead to the irregular growths and hypertrophies referred to; the wounds are kept open and "sore," or

even extended, and there is hardly any limit to the possibilities of damage to the timber thus exposed to a multitude of dangers.

In Fig. 34 is represented a portion of a tree stem affected with "canker": the transverse section shows the periods of growth numbered 1 to 6 from within outwards. When the stem was younger, and the cambium had already developed the zones marked 1 and 2, the cortex suffered some injury near the base of the dead twig, below the figure 1. This injury was aggravated by the ravages of fungus mycelium, which penetrated to the cambium and destroyed it over a small area: in consequence of this, the next periodic zone of wood (marked 3) is of course incomplete over the damaged area, and the cortex and cambium strive to heal over the wound by lip-like callus at the margins. The accomplishment of the healing is prevented, however, by the mycelium, which is continually destroying fresh cells and extending the area of injury: consequently the next zone of wood (4 in the figure) extends even a shorter distance round the stem than this one, and so on with 5 and 6, the cambium being now restricted to less than half the circumference of the stem—*i.e.* from *D* to *D*, and the same with the living cortex. Of course the injured area extends upwards and downwards also, as shown by the lips of

the healing tissue. As soon as the injury extends all round, the stem dies—it is, in fact, ringed. It is also interesting to note that the zones 4 and 5 (and the same would be true of 6 when completed) are thicker than they would have been normally: this is partly due to release from pressure, and partly to a concentrated supply of nutritive materials, due to the stimulating action of the fungus.

Much confusion still exists between the various kinds of "canker": some of them undoubtedly are due to frost or to the intense heat of direct insolation; these are, as a rule, capable of treatment more or less simple, and can be healed up. Others, again, can only be freed from the irritating agents (which, by the by, may be insects as well as fungi) by costly and troublesome methods.

I shall only select one case for illustration, as it is typical, and only too well known. As examples of others belonging to the same broad category, I may mention the "canker" of apple-trees, beeches, oaks, hazels, maples, hornbeams, alders, and limes, and many others; and simply pass the remark that whatever the differences in detail in the special cases, the general phenomena and processes of reasoning are the same in all.

Perhaps no timber disease has caused so much

consternation and difference of opinion as the "larch-disease," and even now there is far too little agreement among foresters either as to what they really mean by this term, or as to what causes the malady. The larch, like other timber-trees, is subject to the attacks of various kinds of fungi and insects, in its timber, roots, and leaves; but the well-known larch-disease, which has been spreading itself over Europe during the present century, and which has caused such costly devastation in plantations, is one of the group of cancerous diseases the outward and visible signs of which are manifested in the cortex and young wood.

The appearance presented by a diseased larch-stem is shown in Fig. 35. In the earlier stages of the malady the stem shows dead, slightly sunken patches, *a*, of various sizes on the cortex, and the wood beneath is found to cease growing: it is a fact to be noted that the dead base of a dried-up branch is commonly found in the middle of the patch. The diseased cortex is found to stick to the wood below, instead of peeling off easily with a knife. At the margins of the flattened patch, just where the dead cortex joins the normal living parts, there may frequently be

seen a number of small cup-like fungus fructifications (Fig. 35, *b*), each of which is white or grey on the outside, and lined with orange-yellow. These are the fruit-bodies of a discomycetous fungus called *Peziza Willkommii* (Htg.), and which has at various times, and by various observers, received at least four other names, which we may neglect.

In the spring or early summer, the leaves of the tree are found to turn yellow and wither on several of the twigs or branches, and a flow of resin is seen at the dead patch of cortex. If the case is a bad one, the whole branch or young tree above the diseased place may die and dry up. At the margins of the patch, the edges of the sounder cortex appear to be raised.

As the disease progresses in succeeding years, the merely flattened dead patch becomes a sunken blistered hole from which resin flows: this sinking in of the destroyed tissues is due to the up-growth of the margins of the patch, and it is noticed that the up-growing margin recedes further and further from the centre of the patch. If this goes on, the patch at length extends all round the stem or branch, and the death of all that lies above is then soon brought about, for since the young wood and cambium beneath the dead cortex are also

destroyed, the general effect is eventually to "ring" the tree.

To understand these symptoms better, it is necessary to examine the diseased patch more closely in its various stages. The microscope shows that the dead and dying cortex, cambium, and

FIG. 35.—Portion of stem of a young larch affected with the larch-disease, as indicated by the dead "cancerous" patch of cracked cortex, *a*: at and near the margins of the patch are the small cup-like fructifications of *Peziza Willkommii* (Htg.), which spring from mycelium in the dead and dying cortex and cambium beneath. (After Hess.)

young wood in a small patch, contain the mycelium of the fungus which gives rise to the cup-like fructifications—*Peziza Willkommii*—above referred to (Fig. 35); and it has been proved that, if the spores of this *Peziza* are introduced into the cortex

of a healthy living larch, the mycelium to which they give rise kills the cells of the cortex and cambium, penetrates into the young wood, and causes the development of a patch which every one would recognize as that of the larch-disease. It is thus shown that the fungus is the immediate cause of the patch in which it is found.

The next fact which has been established is that the fungus can only infect the cortex through some wound or injury—such as a crack or puncture—and cannot penetrate the sound bark, &c. Once inside, however, the mycelium extends upwards, downwards, sideways, and inwards, killing and destroying all the tissues, and so inducing the outflow of resin which is so characteristic of the disease. The much-branched, septate, colourless hyphæ can penetrate even as far as the pith, and the destroyed tissues turn brown and dry up.

After destroying a piece of the tissues in the spring, the growth of the mycelium stops in the summer, the dead cortex dries up and sticks to the wood, and the living cortex at the margins of the patch commence to form a thick layer of cork between its living cells and the diseased area.

It is this cork-formation which gives the appearance of a raised rim around the dead patch. It

has long been known that the patches dry up and cease to spread in the dry season. It should be pointed out that it is one of the most general properties of living parenchymatous tissue to form cork-cells at the boundaries of an injury: if a slice is removed from a potato, for instance, the cut surface will be found in a few days with several layers of cork-cells beneath it, and the same occurs at the cut surface of a slip, or a pruned branch,—the "callus" of tissue formed is covered with a layer of cork.

If it is remembered that the cambium and young wood are destroyed beneath the patch, it will be at once clear that in succeeding periods of growth the annual rings of wood will be deficient beneath the patch.

Next year, the cambium in the healthy parts of the stem begins to form another ring; but the fungus mycelium awakens to renewed activity at the same time, and spreads a little further upwards, downwards, and sideways, its hyphæ avoiding the cork-layer and traversing the young wood and cambium below. During this second spring, therefore, a still larger patch of dead tissue—cortex, cambium, and young wood—is formed, and the cork-layer, developed as usual at the edges of the wound,

describes a larger boundary. Moreover, since the cambium around the, as yet, undiseased parts has added a further annual ring—which of course stops at the boundaries of the diseased patch—the centre of the patch is yet more depressed (cf. Fig. 34).

And so matters go on, year after year, the local injury to the timber increasing, and ultimately seriously affecting, or even bringing to an end, the life of the tree.

At the margins of the diseased patches, as said, the fungus at length sends out its fructifications. These appear at first as very minute cushions of mycelium, from which the cup-like bodies with an orange-coloured lining arise: the structure of this fructification is best seen from the illustration (Fig. 36, A). The orange-red lining (*h*) is really composed of innumerable minute tubular sacs, each of which is termed an *ascus*, and contains eight small spores: as seen in the figure (Fig. 36, B), these asci stand upright like the pile of velvet lining the cup. They are formed in enormous numbers, and go on ripening and scattering the spores, which they do forcibly, day after day. There are many interesting details connected with the development and structure of these fructifications and

spores; but we may pass over these particulars here, the chief point for the moment being that

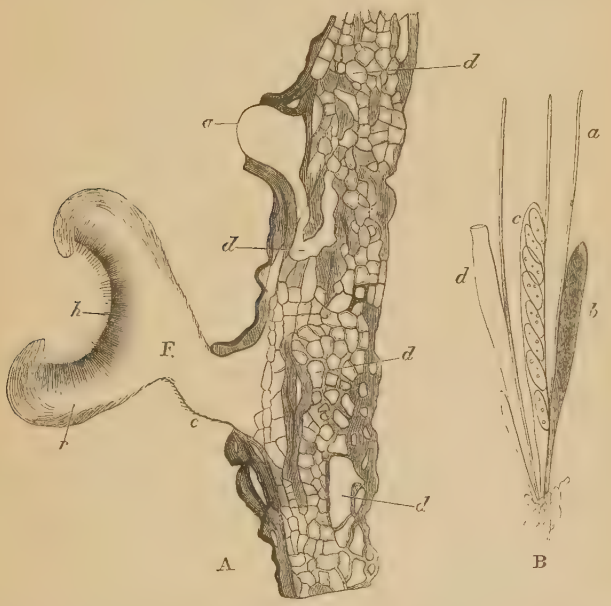

FIG. 36.—A, vertical section (magnified) through the dead cortex of a larch, infected with the mycelium (*d*) of *Peziza Willkommii* (Htg.), which is developing its fructifications (*a* and *F*). The mycelium fills up the gaps in the cortex, *d*, with a white felt-work. *a* is a boss-like cushion of this felt-work bursting forth to become a cup-like fructification; *F*, the mature *Peziza* fructification (in section); *c*, its stalk; *r*, the margins of the cup; *h*, the layer of spore-sacs (*asci*). B, four of the asci from *h*, very highly magnified. *a*, hair-like barren filaments between the sacs; *c*, a fully-developed ascus, containing the eight spores; *d*, an ascus emptied of spores (they have escaped through the hole at the apex); *b*, a young ascus in which the spores are not yet formed: to the left below is a small one still younger. (After Hartig and Willkomm.)

very large numbers of the minute spores are formed, and scattered by the wind, rain, animals, &c. More-

over, as already stated, it has been shown by experiments that the spores will infect the stem of the larch if they are introduced into a wound; but it is important to notice that the fungus cannot penetrate the sound cortex.

It now remains for us to see if, in the natural course of events, infection of the larch can take place to any great extent; for, unless this is the case, we cannot reconcile the above peculiarities of the fungus with the prevalence of the disease.

It must be borne in mind that the larch is an Alpine tree, growing naturally at an elevation of from about 3000 to 6000 feet above sea level, and even more. In its native heights, both the larch-disease and *Peziza Willkommii* occur associated as we have described them, but the malady does not become epidemic, as it has done in the valleys and plains of Europe.

Several insect-enemies of the larch are known, some of which feed on the buds, and others on the leaves, &c.: it is not impossible that insect-wounds may serve occasionally as points of entry for the fungus.

But attention should be directed to the remark made when describing the symptoms of the disease—namely, that a dead branch often springs from near

the centre of the patch. Now it is a well-known fact in the hill-forests of Switzerland, Germany, Austria, &c., that heavy falls of snow often load the branches until they bend down to the ground, and the bark in the upper angle where the branch joins the stem is ruptured; similar cracks are also caused by the bending down of the branches under the weight of water condensed from mists, &c. If a spore alighted near such a place, the rain would wash it into the crevice, and it would germinate in the moisture always apt to accumulate there. This certainly accounts very completely for the situation of the dead branch, which of course would at once suffer from the mycelium. Another way in which such wounds as would give access to the parasite might arise, is from the blows of hailstones on the still young and tender cortex.

But probably the most common source of the crevices or wounds by which the fungus gains an entry is frost; and to understand this we must say a few words as to what is known of the larch at home in its native Alps.

It is well known, since Hartig drew attention to the fact, that in the high regions of the Alps the trees begin to put forth their shoots very late: the larch in the lowlands of Germany and the British

Isles often begins to shoot at the end of March or beginning of April, whereas in the mountains it may be devoid of leaves in May. This is because the transition from winter to spring is very sudden on high slopes, whereas in the lowlands and valleys it may be very gradual. The consequence is that in the Alps, when the buds once begin to open they do this rapidly and vigorously, and the tender leaves and shoots are quickly formed and soon harden beyond the reach of those late spring frosts which do so much damage in our country: in the lowlands, on the contrary, the leaves slowly develop at a time when late frosts are very apt to recur at night, and they are for several weeks exposed to this danger; and if a sharp frost does come, the chances are that not only will the first output of tender leaves be killed off, but the whole shoot suffers, and frost-wounds are formed in the young cortex.

Another point comes into consideration also. In warm damp valleys the whole tree is apt to be more watery, and it is well known that the soft tissues, like the cortex, suffer more from frost when filled with watery sap, than do harder, drier, more matured ones. It has been shown, according to Sorauer, that dead patches, exactly like those which

characterize the larch-disease in its early stages, can be artificially produced by exposing the stem to temperatures below zero, so as to freeze the water in the cells.

Given the above conditions for producing frost-wounds, then, and the presence of spores of *Peziza Willkommii*, there is no difficulty in explaining the well-known phenomena of the larch-disease.

But Hartig has brought to light some other facts of great importance in considering this admittedly complex question. We have already stated that the *Peziza* does occur at the margins of the wounds in trees growing in the Alps where the larch is native. In these higher regions, however, the air is usually relatively dry during periods of active growth, and the young fructifications of the fungus are particularly sensitive to drought; consequently even when many scattered trees are affected, the cups developed at the edges of the wounds are apt either to dry up altogether, or to produce relatively few spores, and these spores have fewer chances of germinating. In fact, the fungus enjoys at best a sporadic existence, chiefly at the bases of trees where the herbage ensures a certain degree of dampness.

When the larch was brought down to the plains and valleys, however, and planted in all directions

over large areas, the *Peziza* was also brought with it; but it will be clear from the foregoing discussion that the climatic conditions were now proportionally raised in favour of the fungus, and lowered to the disadvantage of the larch. Plantations in damp valleys, or in the neighbourhood of the sea, or of large lakes, were especially calculated to suffer from frost, and the damp air favoured the propagation of the fungus, and the disease tended to become epidemic. The enormous traffic in larch plants also shows how man too did his share in spreading the epidemic; and in fact the whole story of the larch-disease is of peculiar interest biologically, as illustrating the risks we run every day in trusting to the chapter of accidents to see us safely through any planting undertaking, no matter how great the stake at issue, or how ruthless the interference with those complex biological and physical conditions which always play such an important part in keeping the balance in the struggle for existence between all organisms living together.

Let us now very shortly see what are the chief lessons taught us by the bitter and costly experience which the larch-disease brought to foresters. It is evident that the larch should not be planted at all in low-lying situations exposed to late frosts; and

even in more favoured valleys experience points to the advantage of mixing it with other trees: large areas of pure larch are planted at enormous risk in the lowlands.

As to the treatment of trees already diseased, it is possible (when it is worth while) to remove diseased branches from trees of which the trunk and crown are healthy, but it hardly needs mention that such diseased branches must be burnt at once. As regards trees with the stems diseased—in those cases where the patches are large, and much resin is flowing from the wounds, experience points to the advisability of cutting them down. In those cases where the tree is already very large, and the diseased wound but small, it may be expedient to let them alone: theoretically they ought to go, or at any rate the diseased tissues be excised and burnt: but it seems to be proved that such a tree may go on forming timber for many years before the wound will spread far enough to reduce the annual increment below the limits of profit, and we all know the view a practical forester will take of such a case. At the same time, it is the duty of the man of science to point out that even such a tree is a source of danger to its neighbours.

CHAPTER XI.

LEAVES, AND LEAF DISEASES.

If the leaves are stripped from a timber-tree early in the summer, or during their young conditions in the spring, the layer of wood produced in the current year—and probably even that formed next year—will be poor and thin. This is simply a fact of observation, and does not depend on what agent deprives the tree of its leaves. Those oaks which suffered so greatly from the ravages of certain tiny caterpillars during the summer of 1887—many of them having all their leaves eaten away before July—will have recorded the disaster by a thin annual ring of wood: it is true the more vigorous trees produced (at the expense of what stores of food materials remained over) a second crop of leaves in August, and so no doubt the zone of wood will prove to be a thin double one, but it was at the expense of the next year's buds.

Now there are very many foes which injure the leaves of our timber trees, and I wish to show, as clearly as possible in a short chapter, how it comes about that injury to the leaves means injury to the timber. The sum total of the matter is that the substances which are to be sent down to the cambium, and converted through its agency into wood, are produced in the cells of the leaves: consequently, from our point of view, when an insect or a fungus consumes the substance of the leaves, it consumes timber in prospective. Similarly, when the leaves are removed from a tree by any agent whatever, the latter is robbed in advance of timber. A leaf, generally speaking, is an extended, flattened appendage of a branch, covered by a continuation of the epidermis of the branch, and containing a continuation of its other tissues—the vascular bundles of the branch being continued as the venation, and the cellular cortex reappearing as the green soft tissue of the leaf. The epidermis of the leaf is so pieced at hundreds of thousands of nearly equi-distant points, that gases can enter into or escape from all its tissues: at these points are the so-called *stomata*, each stoma being a little apparatus which can open and close according to circumstances.

These openings lead into excavations or passages

between the loose cells of the softer leaf-tissue, and if we supposed a very minute creeping organism to enter one of the stomata, it would find itself in a labyrinth of inter-cellular passages: supposing it able to traverse these, it could pass from any part of the leaf to any other between the cells; or it could emerge again from the leaf at thousands of places—other stomata. In traversing the whole of the labyrinth, however, it would pass over many millions of times its own length. Moreover it would find these intercellular passages filled with a varying atmosphere of diffusing gases—oxygen, nitrogen, the vapour of water, and carbon-dioxide being the chief. It would also find the cell-walls which bound the passages damp, with water continuous with the water in the cells. If we suppose our hypothetical traveller threading the mazes of these passages at night, and able to perceive or test the changes which go on, it would find relatively little oxygen and relatively much carbon-dioxide in the damp atmosphere in the passages; whereas in the daylight, if the sun was shining brightly on the leaves, it would find the atmosphere rarer, and relatively little carbon-dioxide present, but an abundance of oxygen. These gases and vapour would be slowly moving in and out at the stomata by diffusion, the evaporation of the watery

vapour especially being quicker on a dry, hot, sunny day.

Inside the cells between which these tortuous passages run, are contained structures which have much to do with these changes. Each of the cells I am considering contains a lining of protoplasm, in which a nucleus, and a number of small protoplasmic granules, coloured green, and called chlorophyll-corpuscles, are embedded : all these are bathed in a watery cell-sap.

Now, putting together in a general manner some of the chief facts which we know about this apparatus, it may be said that the liquid sap inside the cells gives off water to replace that which escapes through the damp cell-walls, and evaporates into the above-named passages and out through the stomata, or at the surface. This evaporation of the water is in itself the cause of a flow of more water from behind, and this flow takes place from the vascular bundles forming the so-called venation of the leaf, coming directly from the wood of the stem. The course of this water, then, is from the soil, through the roots, up the young wood and into the venation of the leaf, and thence it is drawn into the cells we are considering. But this water is not pure water : it contains in solution small quantities of salts of lime, potash, magnesia, nitric,

sulphuric, and phosphoric acids, as well as a little common salt, and traces of one or two other things. It is, in fact, of the nature of ordinary drinking water, which always contains minute quantities of such salts: like drinking water, it also contains gases (oxygen, nitrogen, carbon-dioxide) dissolved in it.

It follows from what has been said that the cell-sap tends to accumulate small increasing quantities of these salts, &c., as the water passes away by evaporation. But we must remember that the living contents —the protoplasm, nucleus, and the green chlorophyll-corpuscles—use up many of these salts for their life-purposes, and other portions pass into the cell-walls.

It will thus be seen that the green chlorophyll-corpuscles are bathed by a fluid cell-sap, the dissolved gaseous and mineral contents of which are continually changing, even apart from the alterations which the life-processes of the living contents of the cell themselves entail. We may say that the chlorophyll-corpuscles find at their disposal in the cell-sap, with which they are more or less in direct contact, traces of salts, oxygen, carbon-dioxide, and of course water, consisting of hydrogen and oxygen.

Now we have the best possible reasons for knowing that some such changes as the following occur in these chlorophyll-corpuscles, provided they are exposed to

sunlight : they take up carbon-dioxide and water, and traces of minerals, and by means of a molecular mechanism which is as yet unexplained in detail, they perform the astonishing feat—for it represents an astonishing transformation when regarded chemically and physically—of tearing asunder, by the aid of the light, the carbon, hydrogen, and oxygen of the carbon-dioxide and water, and rearranging these elements in part so as to form a much more complex body—starch, or an allied compound, oxygen being at the same time set free.

. It is of course not part of my present task to trace these physiological processes in detail, or to bring forward the experimental evidence on which our knowledge of them is based. It must suffice to state that these compounds, starch and allied substances, do not remain in the chlorophyll-corpuscles, but become dissolved and carried away through certain channels in the phloem of the vascular bundles of the venation, and thence pass to wherever they are to be employed as food. The chemical form in which these substances pass from one cell to another in solution is chiefly that of grape-sugar, and it is a comparatively easy observation to make that the cells so often referred to contain such sugar in their sap.

We are only concerned at present with the fate of

a portion—but a very large portion—of this starch and sugar: we can trace them down the vascular bundles of the venation, through the leaf-stalk, into the cortex, and eventually to the cambium-cells; and it is necessary to be quite clear on the following points: (1) the cambium-cells, like all other living cells which contain no chlorophyll, need to be supplied with such foods as sugar, starch, &c., or they starve and perish; (2) since these foods are prepared, as we have seen, in the leaves, and in the leaves only, it is obvious that the vigour and well-being of the cambium depend on the functional activity of the leaves.

We have already seen how the cambium-cells give rise to the young wood, and thus it will be clear how the formation of timber is dependent on the functional activity of the leaves. Moreover, it ought to be mentioned, by the way at least, that it is not only the cambium which depends upon the leaves for its supplies—all the roots, young buds, flowers, and fruits, &c., as well as the cortex and cork-forming tissues, are competitors for the food supply. Now it is clear that if we starve the buds there will be fewer leaves developed in the following year, and so next year's cambium will again suffer, and so on.

I have by no means traced all the details of even the first ramifications of the complex network of

correlations implied by this competition of the various organs and tissues for the food supplies from the leaves; but probably the following proposition will be generally clear:—If the leaves are stripped, the cambium suffers starvation to a greater or less extent, depending on the intensity of its competition with other tissues, &c.; of course a starved cambium will form less wood, and, it may be added, the timber will be poorer.

Again, even if the leaves are not stripped quickly from the tree, but the effect of some external agent is to shorten their period of activity; or to occupy space, on or in them, and so diminish the amount of leaf-surface exposed to the light and air; or to block up their stomata, the points of egress and ingress for gases and water; or to steal the contents of the cells —contents which should normally be passed on for the growth, &c., of other parts of the tree—in all or any of these ways injury to the timber may accrue from the action of the agent in question. Now there are numbers of parasitic fungi which do all these things, and when they obtain a hold on pure plantations or forests, they may do immense injury before their presence is detected by any one not familiar with their appearance and life-histories.

The great difficulty to the practical forester who

attempts to deal with these "leaf diseases" is at least twofold; for not only are the leaves so numerous and so out of reach that he can scarcely entertain the idea of doing anything directly to them, but (and this is by no means so clearly apprehended as it should be) they stay on the tree but a short time as a rule, and when they fall are a continual source of re-infection, because the spores of the fungi are developed on them. It is a curious fact that those fungi which are known to affect the leaves of forest-trees nearly all belong to two highly-developed groups—the Uredineæ and the Ascomycetes—and the remarkable biological adaptations which these parasites exhibit for attacking or entering the leaves, passing through periods of danger, and so on, are nearly as various (and one might almost say ingenious) as they are numerous. Some of them, such as the *Erysipheæ* or mildews on beeches, oaks, birches, ashes, &c., only form small external patches on the leaves, and do little if any harm where the leaf-crown is large and active; others, such as many of the very numerous *Sphæriaceæ* and their allies, which form small dark-coloured flecks and spots on leaves, may also be looked upon as taking only a slight tax from the leaves. Even in these cases, however, when the diseases become epidemic in certain wet seasons, considerable damage may accrue, because

two chief causes (and many minor ones) are co-operating to favour the fungus in the struggle for existence: in the first place, a continuously wet summer means loss of sunlight and diminished transpiration, &c., to the leaves, and so they form smaller quantities of food materials; and secondly, the damp in the atmosphere and leaves favours the fungi proportionally more than the leaves, and so they destroy and occupy larger areas of leaf surface.

It should be mentioned here, by the way, that all leaves of all trees are apt to have fungi on them in a wet summer, but many of these are only spreading their mycelia in all directions over the epidermis, in preparation, as it were, for the fall of the leaf: they are saprophytes which feed on the dead fallen leaves, but cannot enter into them while they are yet alive. In some cases, however, this preparation for the fall is strikingly suggestive of adaptation towards becoming parasites. I will quote one instance only in illustration of this. On the leaves of certain trees in Ceylon, there was always to be found in the rainy season the much-branched mycelium of a minute *Sphæria*: this formed enormous numbers of branches, which, on the older leaves, were found to stop short over the stomata, and to form eventually a four-celled spore-like body just blocking up each stoma on which it rested. So

long as the leaf remained living on the tree, nothing further occurred; but wherever a part of the leaf died, or when the leaf fell moribund on the ground, these spore-like bodies at once began to send hyphæ into the dying tissue, and thus obtained an early place in the struggle for existence among the saprophytes which finished the destruction of the cells and tissues of the leaf.

There is another group of fungi, the *Capnodieæ*, which form sooty black patches on the leaves, and which are very apt to increase to a dangerous extent on leaves in damp shady situations; these have no connection with the well-known black patches of *Rhytisma* from which the leaves of our maples are rarely free. This last fungus is a true parasite, its mycelium penetrates into the leaf tissues, and forms large black patches, in and near which the cells of the leaf either live for the benefit of the fungus alone, or entirely succumb to its ravages: after the leaf has fallen, the fungus forms its spores. Nevertheless, although we have gone a step further in destructiveness, foresters deny that much harm is done to the trees—no doubt because the foliage of the maples is so very abundant. Willows, pines, and firs suffer from allied forms of fungi.

But it is among the group of the *Uredineæ*, or rusts,

that we find the most extraordinary cases of parasitism, and since some of these exhibit the most highly developed and complex adaptations known to us, I propose to select one of them as the type of these so-called "leaf diseases." This form is *Coleosporium Senecionis* (*Peridermium Pini*), rendered classical by the reseaches of several excellent botanists.

It is true, *Coleosporium Senecionis* is not in some respects the most dangerous of these fungi—or, rather, it has not hitherto been found to be so—but in view of the acknowledged fact that foresters have not as yet been able to devise practical measures against the ravages of these numerous rust-fungi, and since we are still very ignorant of the details of the biology of most of them, it seems advisable to choose for illustration a form which shows in a distinct manner the complexities of the subject, so that those interested may see in what directions botanists may look for new results. That the story of this fungus is both complicated and of great biological interest will be sufficiently evident from the mere recital of what we know concerning it.

CHAPTER XII.

PINE-BLISTER.

Coleosporium Senecionis (*Peridermium Pini*).

In the months of April and May, the younger needle-like leaves of the Scotch pine are occasionally seen to have assumed a yellow tinge, and on closer examination this change in colour, from green to yellow, is seen to be due to the development of what look like small orange-coloured vesicles or blisters standing off from the surface of the epidermis, and which have in fact burst through from the interior of the leaf (Fig. 37). Between these larger orange-yellow blisters the lens shows certain smaller brownish or almost black specks. Each of the vesicular swellings is a form of fungus-fructification known as an *Æcidium*, and each of the smaller specks is a fungus-structure called a *Spermogonium*, and both of these bodies are

developed from a mycelium in the tissues of the leaf. I must employ these technical terms, but will explain them more in detail shortly: the

FIG. 37.—To the left is a pair of leaves of the Scotch pine, with the blister-like *Æcidia*. *a*, of *Peridermium Pini* (var. *acicola*) projecting from their tissues: these blisters are orange-yellow in colour, and contain spores, as shown in Fig. 38. Between the blisters are the minute *spermogonia*, *b*. To the right is a small branch, killed at *a a a* by *Peridermium Pini* (var. *corticola*), the blister-like yellow *Æcidia* of the fungus being very conspicuous. (Reduced, after Hartig.)

point to be attended to for the moment is that this fungus in the leaf has long been known under the name of *Peridermium Pini* (var. *acicola*,

i.e. the variety which lives upon the needle-like leaves).

On the younger branches of the Scotch pine, the Weymouth pine, the Austrian pine, and some others, there may also be seen in May and June similar but larger bladder-like orange vesicles

FIG. 38.—Blisters (*Æcidia*) of *Peridermium Pini* (var. *corticola*) on a branch of the Scotch pine: some of the *Æcidia* have already burst at the apex and scattered their spores, *b*, *b*; the others are still intact. (Natural size, after Hess.)

(*Æcidia*) bursting through the cortex (Figs. 37 and 38); and here, again, careful examination shows the darker smaller *spermogonia* in patches between the *æcidia*. These also arise from a fungus-mycelium in the tissues of the cortex, whence the fungus was named *Peridermium Pini* (var.

corticola). It is thus seen that the fungus *Peridermium Pini* was regarded as a parasite of pines, and that it possessed two varieties, one inhabiting the leaves and the other the cortex: the "varieties" were so considered, because certain trivial differences were found in the minute structure of the *æcidia*

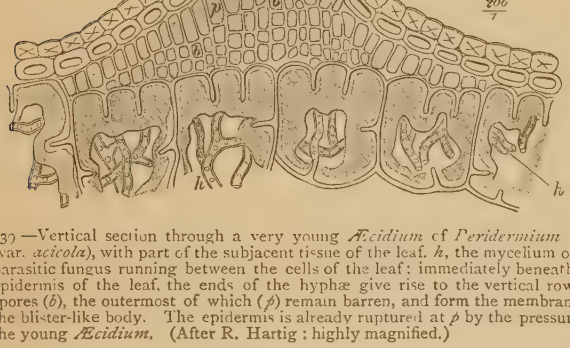

FIG. 39.—Vertical section through a very young *Æcidium* of *Peridermium Pini* (var. *acicola*), with part of the subjacent tissue of the leaf. *h*, the mycelium of the parasitic fungus running between the cells of the leaf: immediately beneath the epidermis of the leaf, the ends of the hyphæ give rise to the vertical rows of spores (*b*), the outermost of which (*p*) remain barren, and form the membrane of the blister-like body. The epidermis is already ruptured at *p* by the pressure of the young *Æcidium*. (After R. Hartig: highly magnified.)

and *spermogonia*. The disease may be popularly denoted "Pine-blister."

If we cut thin vertical sections through a leaf and one of the smallest blisters or *æcidia*, and examine the latter with the microscope, it will be found to consist of a mass of spores arranged in vertical rows, each row springing from a branch of the

mycelium: the outermost of these spores—*i.e.* those which form a compact layer close beneath the epidermis—remain barren, and serve as a kind of membrane covering the rest (Fig. 39, *p*). It is this membrane which protrudes like a blister from the tissues. The hyphæ of the fungus are seen running in all directions between the cells of the leaf-tissue, and as they rise up and form the vertical chains of spores, the pressure gradually forces up the epidermis of the leaf, bursts it, and the mass of orange-yellow powdery spores protrude to the exterior, enveloped in the aforesaid membrane of contiguous barren spores. If we examine older *æcidia* (Fig. 38, *b*) it will be found that this membrane at length bursts also, and the spores escape.

Similar sections across a *spermogonium* exhibit a structure which differs slightly from the above. Here also the hyphæ in the leaf turn upwards, and send delicate branches in a converging crowd beneath the epidermis; the latter gives way beneath the pressure, and the free tips of the hyphæ constrict off extremely minute spore-like bodies. These minute bodies are termed *Spermatia*, and I shall say no more about them after remarking that they are quite barren, and that similar sterile bodies are known to occur in very many of the fungi belonging to this and other groups.

Sections through the *æcidia* and *spermogonia* on the cortex present structures so similar, except in minute details which could only be explained by lengthy descriptions and many illustrations, that I shall not dwell upon them; simply reminding the reader that the resemblances are so striking that systematic mycologists have long referred them to a mere variety of the same fungus.

Now as to the kind and amount of damage caused by the ravages of these two forms of fungus.

In the leaves, the mycelium is found running between the cells (Fig. 39, *h*), and absorbing or destroying their contents: since the leaves do not fall the first season, and the mycelium remains living in their tissues well into the second year, it is generally accepted that it does little harm. At the same time, it is evident that, if very many leaves are being thus taxed by the fungus, they cannot be supplying the tree with food materials in such quantities as if the leaves were intact. However, the fungus is remarkable in this respect—that it lives and grows for a year or two in the leaves, and does not (as so many of its allies do) kill them after a few weeks. It is also stated that only young pines are badly attacked by this form: it is rare to find *æcidia* on trees more than twenty years or so old.

Much more disastrous results can be traced directly to the action of the mycelium in the cortex. The hyphæ grow and branch between the green cells of the true cortex, as well as in the bast-tissues beneath, and even make their way into the medullary rays and resin-canals in the woods, though not very deep. Short branches of the hyphæ pierce the cells, and consume their starch and other contents, causing a large outflow of resin, which soaks into the wood or exudes from the bark. It is probable that this effusion of turpentine into the tissues of the wood cambium, and cortex, has much to do with the drying up of the parts above the attacked portion of the stem: the tissues shrivel up and die, the turpentine in the canals slowly sinking down into the injured region. The drying up would of course occur in any case if the conducting portions are steeped in turpentine, which prevents the conduction of water from below.

The mycelium lives for years in the cortex, and may be found killing the young tissues just formed from the cambium during the early summer: of course the annual ring of wood, &c., is here impoverished. If the mycelium is confined to one side of the stem, a flat or depressed spreading wound arises; if this extends all round, the parts above must die.

When fairly thick stems or branches have the mycelium on one side only, the cambium is injured locally, and the thickening is of course partial. The annual rings are formed as usual on the opposite side of the stem, where the cambium is still intact, or they are even thicker than usual, because the cambium there diverts to itself more than the normal share of food-substances: where the mycelium exists, however, the cambium is destroyed, and no thickening layer is formed. From this cause arise cancerous malformations which are very common in pine-woods (Fig. 40).

Putting everything together, it is not difficult to explain the symptoms of the disease. The struggle between the mycelium on the one hand, which tries to extend all round in the cortex, and the tree itself, on the other, as it tries to repair the mischief, will end in the triumph of the fungus as soon as its ravages extend so far as to cut off the water-supply to the parts above: this will occur as soon as the mycelium extends all round the cortex, or even sooner if the effusion of turpentine hastens the blocking up of the channels. This may take many years to accomplish.

So far, and taking into account the enormous spread of this disastrous disease, the most obvious

measures seem to be, to cut down the diseased trees —of course this should be done in the winter, or at least before the spores come—and use the timber as best may be ; but we must first see whether such a suggestion needs modifying, after learning more about the fungus and its habits. It appears clear, at any rate, however, that every diseased tree removed means a source of æcidiospores the less.

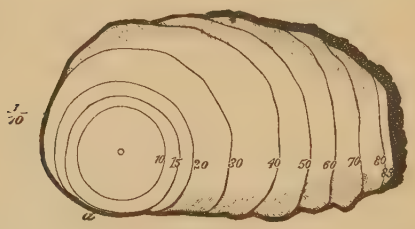

FIG. 40.—Section across an old pine-stem in the cancerous region injured by *Peridermium Pini* (var. *corticola*). As shown by the figures, the stem was fifteen years old when the ravages of the fungus began to affect the cambium near *a*. The mycelium, spreading in the cortex and cambium on all sides, gradually restricted the action of the latter more and more: at thirty years old, the still sound cambium only extended half-way round the stem—no wood being developed on the opposite side. By the time the tree was eighty years old, only the small area of cambium indicated by the thin line marked 80 was still alive; and soon afterwards the stem was completely "ringed," and dead, all the tissues being suffused with resin. (After Hartig.)

Probably every one knows the common groundsel (*Senecio vulgaris*) which abounds all over Britain and the Continent, and no doubt many of my readers are acquainted with other species of the same genus to which the groundsel belongs, and especially with the ragwort (*Senecio Jacobæa*). It has long been known

that the leaves of these plants, and of several allied species, are attacked by a fungus, the mycelium of which spreads in the leaf-passages, and gives rise to powdery masses of orange-yellow spores, arranged in vertical rows beneath the stomata: these powdery masses of spores burst forth through the epidermis, but are not clothed by any covering, such as the *æcidia* of *Peridermium Pini*, for instance. These groups of yellow spores burst forth in irregular powdery patches, scattered over the under sides of the leaves in July and August: towards the end of the summer a slightly different form of spore, but similarly arranged, springs from the same mycelium on the same patches. From the differences in their form, time of appearance, and (as we shall see) functions, these two kinds of spores have received different names. Those first produced have numerous papillæ on them, and were called *Uredospores*, from their analogies with the uredospore of the rust of wheat; the second kind of spore is smooth, and is called the *Teleutospores*, also from analogies with the spores produced in the late summer by the wheat-rust. The fungus which produces these uredospores and teleutospores was named, and has been long distinguished as, *Coleosporium Senecionis* (Pers.). We are not immediately interested in the damage done

by this parasite to the weeds which it infests, and at any rate we are not called upon to deplore its destructive action on these garden pests: it is sufficient to point out that the influence of the mycelium is to shorten the lives of the leaves, and to rob the plant of food material in the way referred to generally in the last chapter.

What we are here more directly interested in is the following. A few years ago Wolff showed that if the spores from the *Æcidia* of *Peridermium Pini* are sown on the leaf of *Senecio*, the germinal hyphæ which grow out from the spores *enter the stomata of the Senecio leaf, and there develop into the fungus called Coleosporium Senecionis.* In other words, the fungus growing in the cortex of the pine, and that parasitic on the leaves of the groundsel and its allies, are one and the same: it spends part of its life on the tree and the other part on the herb.

If I left the matter stated only in this bald manner it is probable that few of my readers would believe the wonder. But, as a matter of fact, this phenomenon, on the one hand, is by no means a solitary instance, for we know many of these fungi which require two host-plants in order to complete their life-history; and, on the other hand, several observers of the highest rank have repeated Wolff's experiment

and found his results correct. Hartig, for instance, to whose indefatigable and ingenious researches we owe most that is known of the disease caused by the *Peridermium*, has confirmed Wolff's results; and in

FIG. 41.—A spore of *Peridermium Pini* germinating. It puts forth the long, branched germinal hyphæ on the damp surface of a leaf of *Senecio*, and one of the branches enters a stoma, and forms a mycelium in the leaf: after some time, the mycelium gives rise to the uredospores and teleutospores of *Coleosporium Senecionis*. (After Tulasne: highly magnified.)

this country Mr. Plowright has successfully repeated the culture.

It was to the brilliant researches of the late Prof. De Bary that we owe the first recognition of this

remarkable phenomenon of *heteræcism—i.e.* the inhabiting more than one host—of the fungi. De Bary proved that the old idea of the farmer, that the rust is very apt to appear on wheat growing in the neighbourhood of barberry-bushes, was no fable; but, on the contrary, that the yellow *Æcidium* on the barberry is a phrase in the life-history of fungus causing the wheat-rust. Many other cases are now known, *e.g.* the *Æcidium abietinum*, on the spruce firs in the Alps, passes the other part of its life on the Rhododendrons of the same region. Another well-known example is that of the fungus *Gymnosporangium*, which injures the wood of junipers: Oersted first proved that the other part of its life is spent on the leaves of certain Rosaceæ, and his discovery has been repeatedly confirmed. I have myself observed the following confirmation of this. The stems of the junipers so common in the neighbourhood of Silverdale (near Morecambe Bay) used to be distorted with *Gymnosporangium*, and covered with the *teleutospores* of this fungus every spring: in July all the hawthorn hedges in the neighbourhood had their leaves covered with the Æcidium form (formerly called *Ræstelia*), and it was quite easy to show that the fungus on the hawthorn leaves was produced by sowing the *Gymnosporangium*

spores on them. Many other well-established cases of similar heterœcism could be quoted.

But we must return to the *Peridermium Pini*. It will be remembered that I expressed myself somewhat cautiously regarding the *Peridermium* on the leaves (var. *acicola*). It appears that there is need for further investigations into the life-history of this form, for it has been thought more than probable that it is not a mere variety of the other, but a totally different species.

Only so lately as 1883, however, Wolff succeeded in infecting the leaves of *Senecio* with the spores of *Peridermium Pini* (*acicola*), and developing the *Coleosporium*, thus showing that both the varieties belong to the same fungus.

It will be seen from the foregoing that in the study of the biological relationships between any one plant which we happen to value because it produces timber, and any other which grows in the neighbourhood there may be (and there often is) a series of problems fraught with interest so deep scientifically, and so important economically, that one would suppose no efforts would be spared to investigate them: no doubt it will be seen as time progresses that what occasionally looks like apathy with regard to these matters is in reality only apparent indifference due to want of information.

Returning once more to the particular case in question, it is obvious that our new knowledge points to the desirability of keeping the seed-beds and nurseries especially clean from groundsel and weeds of that description: on the one hand, such weeds are noxious in themselves, and on the other they harbour the *Coleosporium* form of the fungus *Peridermium* under the best conditions for infection. It may be added that it is known that the fungus can go on being reproduced by the *uredospores* on the groundsel-plants which live through the winter.

CHAPTER XIII.

THE "DAMPING OFF" OF SEEDLING TREES: *Phytophthora omnivora.*

IT may possibly be objected that the subject of the present chapter cannot properly be brought under the title of this book, since the disease to be discussed is not a disease of timber *in esse* but only of timber *in posse;* nevertheless, while acknowledging the validity of the objection, I submit that in view of the fact that the malady to be described effects such important damage to the young plants of several of our timber-trees, and that it is a type of a somewhat large class of diseases, the slight inconsistency in the wording of the general title may be overlooked.

It has long been known to forest nurserymen that, when the seedling beeches first appear above the ground, large numbers of them die off in a peculiar manner—they are frequently said to "damp off" or

to "rot off." A large class of diseases of this kind is only too familiar, in its effects, to cultivators in all parts of the world. Every gardener probably knows how crowded seedlings suffer, especially if kept a trifle too damp or too shaded, and I have a distinct recollection of the havoc caused by the "damping off" of young and valuable Cinchona seedlings in Ceylon.

In the vast majority of the cases examined, the "damping off" of seedlings is due to the ravages of fungi belonging to several genera of the same family as the one (*Phytophthora infestans*) which causes the dreaded potato disease—*i.e.* to the family of the Peronosporeæ—and since the particular species (*Phytophthora omnivora*) which causes the wholesale destruction of the seedlings of the beech is widely distributed, and brings disaster to many other plants; and since, moreover, it has been thoroughly examined by various observers, including De Bary, Hartig, Cohn, and others, I propose to describe it as a type of the similar forms scattered all over the world.

It should be premised that, when speaking of this disease, it is not intended to include those cases of literal damping off caused by stagnant water in ill-drained seed-beds, or those cases where insufficient light causes the long-drawn, pale seedlings to perish from want of those nutrient substances which it can

only obtain, after a certain stage of germination, by means of the normal activity of its own green cotyledons or leaves, properly exposed to light, air, &c. At the same time, it is not to be forgotten that, *as conditions which favour the spread of the disease to be described*, the above factors and others of equal moment have to be taken into account: which is indeed merely part of a more general statement, viz. that, to understand the cause and progress of a disease, we must learn all we can about the conditions to which the organisms are exposed, as well as the structure, &c., of the organisms themselves.

First, a few words as to the general symptoms of the disease in question. In the seed-beds, it is often first noticeable in that patches of seedlings here and there begin to fall over, as if they had been bitten or cut where the young stem and root join, at the surface of the ground: on pulling up one of the injured seedlings, the "collar," or region common to stem and root, will be found to be blackened, and either rotten or shrivelled, according to the dampness or dryness of the surface of the soil. Sometimes the whole of the young root will be rotting off before the first true leaves have emerged from between the cotyledons; in other cases, the "collar" only is rotten, or shrivelled, and the weight of the parts above ground causes them

to fall prostrate on the surface of the soil; in yet others, the lower parts of the stem of the older seedling may be blackened, and dark flecks appear on the cotyledons and young leaves, which may also turn brown and shrivel up (Fig. 42).

If the weather is moist—*e.g.* during a rainy May or June—the disease may be observed spreading rapidly from a given centre or centres, in ever-widening circles. It has also been noticed that if a moving body passes across a diseased patch into the neighbouring healthy seedlings, the disease in a few hours is observed spreading in its track. It has also been found that if seeds are again sown in the following season in a seed-bed which had previously contained many of the above diseased seedlings, the new seedlings will inevitably be killed by this "damping off." As we shall see shortly, this is because the resting spores of the fungus remain dormant in the soil after the death of the seedlings.

In other words, the disease is infectious, and spreads centrifugally from one diseased seedling to another, or from one crop to another: if the weather is moist and warm—"muggy," as it is often termed—such as often occurs in the cloudy days of a wet May or June, the spread of the disease may be so rapid that every plant in the bed is infected in the course of two or

three days, and the whole sowing reduced to a putrid mass; in drier seasons and soils, the spread of the infection may be slower, and only a patch here and

FIG. 42.—A young beech-seedling attacked by *Phytophthora omnivora*: the moribund tissues in the brown and black patches on the young stem, cotyledons, and leaves, are a prey to the fungus, the mycelium of which is spreading from the different centres. The horizontal line denotes the surface of the soil.

there die off, the diseased parts shrivelling up rather than rotting.

If a diseased beech seedling is lifted, and thin sections of the injured spots placed under the microscope, it will be found that numerous slender colourless fungus-filaments are running between the cells of the tissues, branching and twisting in all directions. Each of these fungus-filaments is termed a hypha, and it consists of a sort of fine cylindrical pipe with very thin membranous walls, and filled with watery protoplasm. These hyphæ possess the power of boring their way in and between the cell-walls of the young beech seedling, and of absorbing from the latter certain of the contents of the cells. This is accomplished by the hyphæ putting forth a number of minute absorbing organs, like suckers, into the cells of the seedling, and these take up substances from the latter: this exhaustion process leads to the death of the cells, and it is easy to see how the destruction of the seedling results when thousands of these hyphæ are at work.

At the outer parts of the diseased spots on the cotyledons or leaves of the seedling, the above-named hyphæ are seen to pass to the epidermis, and make their way to the exterior: this they do either by passing out through the openings of the stomata, or by

simply boring through the cell-walls (Fig. 43). This process of boring through the cell-walls is due to the action of a solvent substance excreted by the growing

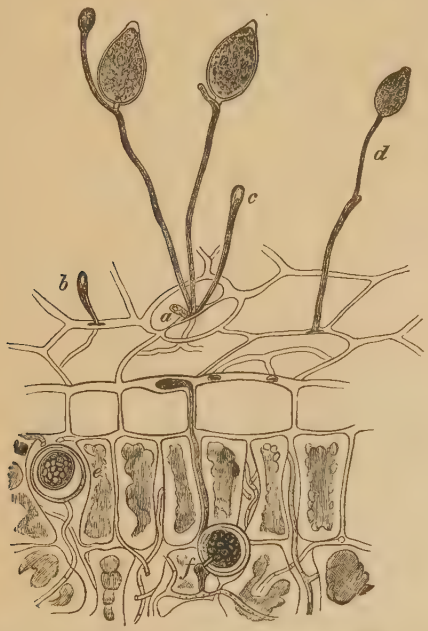

FIG. 43.—Portion of a cotyledon of the beech, infested with *Phytophthora omnivora*: the piece is shown partly in vertical section. The mycelium, spreading between the cells, puts forth aerial hyphæ, which bore between the cells of the epidermis, *b*, and *d*, or emerge from the stomata, *a*, and form conidia at their apices: the various stages of development are shown. On other hyphæ, between the cells of the interior, the oospores are formed in oogonia, *e* and *f*. (Highly magnified.)

tip of the hypha: the protoplasm secretes a ferment, which passes out, and enables the tip to corrode or dissolve away the substance of the cell-walls. It is

also characteristic of these hyphæ that they make their way in the substance of the cell-walls, in what is known as the "middle lamella": in this, and in what follows, they present many points of resemblance to the potato-disease fungus, which is closely allied to *Phytophthora omnivora*.

The hyphæ which project from the epidermis into the damp air proceed to develop certain spores, known as the *conidia*, which are capable of at once germinating and spreading the disease. These conidia are essentially nothing but the swollen ends of branches of these free hyphæ: the ends swell up and large quantities of protoplasm pass into them, and when they have attained a certain size, the pear-shaped bodies fall off, or are blown or knocked off.

Now the points to be emphasized here are, not so much the details of the spore-formation, as the facts that (1) many thousands of these spores[1] may be formed in the course of a day or two in warm, damp weather; and (2) any spore which is carried by wind, rain, or a passing object to a healthy seedling may infect it (in the way to be described) within a few hours, because the spore is capable of beginning to germinate at once in a drop of rain or dew. A little reflection will show

[1] I here use the popular term for them: they are more properly called *Conidia*.

that this explains how it is that the disease is spread in patches from centres, and also why the spread is so rapid in close, damp weather.

When a conidium germinates in a drop of dew for instance, the normal process is as follows. The protoplasm in the interior of the pear-shaped conidium

FIG. 44.—Portion of epidermis of a beech-seedling, on which the conidia of the *Phytophthora* have fallen and burst, *a* and *d*, emitting the motile zoospores, *b*, which soon come to rest and germinate, *c*, by putting forth a minute germinal hypha, *c*, *e*, which penetrates between the cells of the epidermis, *e* and *f*, and forms the mycelium in the tissues beneath. At *d* a zoospore has germinated, without escaping from the conidium. (Highly magnified: partly after De Bary and Hartig.)

becomes divided up into about twenty or thirty little rounded naked masses, each of which is capable of very rapid swimming movements; then the apex of

the conidium bursts, and lets these minute motile zoospores, as they are called, escape (Fig. 44, *a*).

Each zoospore then swims about for from half an hour to several hours in the film of water on the surface of the epidermis, and at length comes to rest somewhere. Let us suppose this to be on a cotyledon, or on the stem or root. In a short time, perhaps half an hour, the little zoospore begins to grow out at one point—or even at more than one—and the protuberance which grows out singly bores its way directly through the cell-wall of the seedling, and forms a cylindrical hypha inside (Fig. 44, *b*, *c*, *e*, *f*): this hypha then branches, and soon proceeds to destroy the cells and tissues of this seedling. The whole process of germination, and the entrance of the fungus into the tissues, up to the time when it in its turn puts out spore-bearing hyphæ again, only occupies about four days during the moist warm weather in May, June, and early in July.

We are now in a position to make a few remarks which will enable practical people to draw helpful conclusions from what has been stated. Let us suppose a seed-bed several feet long and about three feet wide, and containing some thousands of young beech seedlings: then suppose that—by any means whatever—a single conidium of *Phytophthora omnivora*

is carried on to a cotyledon of one of the seedlings. Let us further assume that this occurs one warm evening in May or June. During the night, as the air cools, the cotyledon will be covered with a film or drops of water, and the conidium will germinate and allow, say, thirty zoospores to escape. Now, the average size of a conidium is about 1/400 of an inch long by about 1/700 of an inch broad, and we may take the zoospore as about 1/2000 of an inch in diameter; thus it is easy to see that the film of moisture on the cotyledon is to a zoospore like a pond or a lake to a minnow, and the tiny zoospores, after flitting about in all directions, come to rest at so many distant points on the cotyledon—or some of them may have travelled abroad along the moist stem, or along a contiguous leaf, &c. Before daylight, each of these thirty zoospores may have put forth a filament (Fig. 44, *e*, *f*) which bores between the cells of the cotyledon, and begins to grow and branch in the tissues, destroying those cell-contents which it does not directly absorb, and so producing the discoloured disease-patches referred to. Supposing the weather to remain damp and warm, some of the hyphæ may begin to emerge again from the diseased and dying seedling on the fourth day after infection—or at any rate within the week—and this may go on hour after

hour and day after day for several weeks, each hypha producing two or more conidia within a few hours of its emergence ; hence hundreds of thousands of conidia may be formed in the course of a few days, and if we reflect how light the conidia are, and how their zoospores can flit about to considerable distances, it is not surprising that many of them are shed on to

FIG. 45.—An oogonium and antheridium of *Phytophthora omnivora*. The oogonium is the larger rounded body, borne on a branch of the mycelium: it contains an oosphere, in process of being fertilized by the protoplasm of the antheridium (the smaller body applied to the side of the oogonium). The antheridium has pierced the wall of the oogonium, by means of a fertilizing tube, through which the contents pass into the oosphere, converting the latter into an oospore. (Very highly magnified; after De Bary.)

the surrounding seedlings, to repeat the story. If we further bear in mind that not only every puff of wind, but every drop of rain, every beetle, or fly, or mouse, &c., which shakes the diseased seedling may either shake conidia on to the next nearest seedlings or even carry them further, it is clearly intelligible how the infection is brought about, and spreads through the

seed-bed, gathering strength, as it were, hour by hour.

But, although we have explained the rapid infection from plant to plant, it still remains to see how it is that if we sow the seeds in this bed next year, the seedlings are almost certain to be generally and badly attacked with the disease at a very early stage.

When the fungus-mycelium in the cotyledons and other parts of the diseased seedlings has become fully developed, and has given off thousands of the conidia above described, many of the branches in the dying tissues commence to form another kind of spore altogether, and known as an oospore, or egg-like spore. This spore differs from the conidium in size, shape, and position, as well as in its mode of development and further behaviour, and if it were not that several observers have seen its formation on the same hyphæ as those which give rise to the conidia, it might be doubted by a beginner whether it really belongs to our fungus at all. As it is absolutely certain, however, that the oospore on germination gives rise to the fungus we are considering, the reader may rest satisfied on that point.

The spore in question is formed in a swelling of the free end of a branch of the hypha as follows (Fig. 45). The protoplasm in the rounded end of the hypha

becomes collected into a ball (the egg-cell or *oosphere*) and then a smaller branch with a distinct origin applies itself to the outside of this rounded swelling and pierces its wall by means of a narrow tube: protoplasm from the smaller branch (*antheridium*) is then poured through the tube into the "egg-cell," which thus becomes a fertilized "egg-spore" or *oospore*. This *oospore* then acquires a very hard coating, and possesses the remarkable peculiarity that it may be kept in a dormant state for months and even a year or more before it need germinate: for this reason it is often called a resting spore. It has been found that about 700,000 oospores may be formed in one cotyledon, and a handful of the infected soil has sufficed to kill 8000 seedlings.

Now, when we know this, and reflect that thousands of these *oospores* are formed in the rotting seedlings and are washed into the soil of the seed-bed by the rain, it is intelligible why this seed-bed is infected. If seeds are sown there the next spring, the young seedlings are attacked as soon as they come up. These *oospores* are, in fact, produced in order that the fungus shall not die out as soon as it has exhausted the current year's supply of seedlings; whereas the *conidia*, which soon lose their power of germinating, are the means by which the parasite rapidly extends

itself when the conditions are most favourable for its development and well-being.

It has already been mentioned that other plants besides the beech are destroyed by the ravages of this fungus. Not only has it been found to grow on herbaceous plants, such as *Sempervivum*, *Clarkia*, and many others, but it habitually attacks the seedlings of many timber trees, such as, for instance, those of the spruce and silver firs, the Scotch pine, the Austrian and Weymouth pines, the larch, the maples, and particularly those of the beech.

It is obvious that this makes the question of combating this disease a difficult one, and the matter is by no means simplified when we learn that the fungus can live for a long time in the soil as a saprophyte, and apart from the seedlings. In view of all the facts, let us see, however, if anything can be devised of the nature of precautionary measures. It must at least be conceded that we gain a good deal by knowing so much as we do of the habits of this foe.

In the first place, it will occur to everybody never to use the same seed-bed twice; but it may be added that this precaution need not be taken as applying to anything but seeds and seedlings. Young plants, after the first or second year, are not attacked by the fungus—or rather are attacked in vain, if at all—

and so the old beds may be employed for planting purposes. In the event of a patch of diseased seedlings being found in the seed-bed, as in our illustration quoted above, the procedure is as follows: cover the whole patch with soil as quietly and quickly as possible, for obviously this will be safer than lifting and shaking the spore-laden plantlets. If, however, the sharp eye of an intelligent gardener or forester detects one or two isolated seedlings showing the early stages of the disease, it is possible to remove the single specimens and burn them, care being taken that the fingers, &c., do not rub off spores on to other seedlings.

In the last event, the beds must be looked to every day to see that the disease is not spreading. All undue shading must be removed, and light and air allowed free play during part of the day at least; by such precautions, carefully practised in view of the above facts and their consequences, it is quite feasible to eradicate the disease in cases where ignorant or stupid mismanagement would result in the loss of valuable plants and time. In the case of other seedlings also, much may be done by intelligently applying our knowledge of the disease and its cause. It is not our purpose at present to deal with the diseases of garden plants, &c., but it may be remarked in passing that in the large majority of cases the "damping off"

of seedlings is due to the triumphant development of fungi belonging to the same genus as the one we have been considering, or else to the closely allied genus *Pythium*. In illustration of this I will mention one case only.

It is always possible to obtain well-grown specimens of the fungus *Pythium* by sowing cress seed fairly thick and *keeping the soil well watered and sheltered.* Now what does this mean? Nobody imagines that the fungus arises spontaneously, or is produced in any miraculous manner; and in fact we need not speculate on the matter, for the fact is that by keeping the crowded cress seedlings moist and warm we favour the development of the *Pythium* (spores of which are always there) in somewhat greater proportion than we do the development of the cress. In other words, when the cress is growing normally and happily under proper conditions, it is not because the *Pythium* is absent, but because (under the particular conditions which favour the normal development of healthy cress) it grows and develops spores relatively so slowly that the young cress seedlings have time to grow up out of its reach. The recognition of this struggle for existence on the part of seedlings is of the utmost importance to all who are concerned with the raising of plants.

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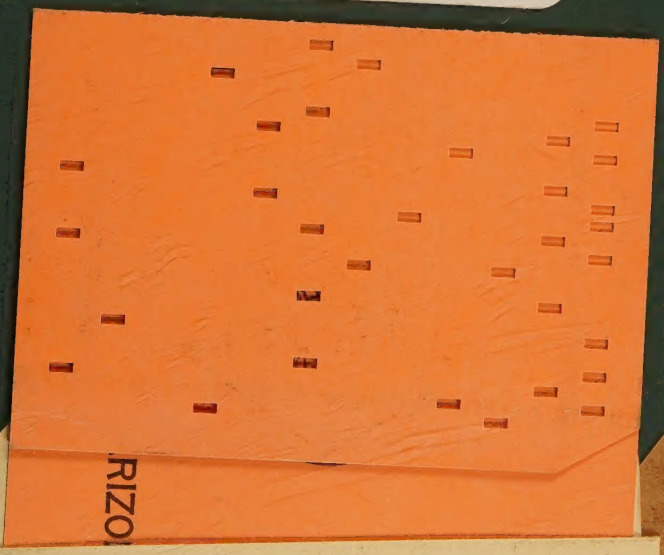
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